

ART XVIII. HYBRIDIZATION AND THE PHYLOGENY OF THE GENUS *PLATYSAMIA*

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(TEXT FIGURES 1-5; CHARTS I-III)

(PLATES XV-XX)

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FOREWORD

It would require too much space to acknowledge individually all of the many persons who have assisted in the work recorded in this paper. The writer wishes to thank those hospitable people who helped him during his survey trips, the many entomologists throughout the United States and Canada who have supplied information and material, and the scientific workers in the University of Pittsburgh and the Carnegie Museum who have generously given their time and advice.

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I. INTRODUCTION

A. THE SELECTION OF THE PROBLEM

The work presented in this paper is a by-product of an investigation into the underlying principles involved in the wing patterns of the Lepidoptera. Hybridization was proposed as a tool with which to pry into the secrets of this tremendously varied expression of nature's art. The apparent duplication of homologous markings in a hybrid between *Mimas tilia* and *Smerinthus ocellata* suggested this line of attack. Accordingly a considerable number of species belonging to the families Saturniidae and Sphingidae were used in attempts to produce hybrids. The ease with which cross matings were obtained in the genus *Platysamia* (Grote) = *Samia* (authors) of the former family led to speculation as to what would happen if the ranges of two species should overlap. A careful search of the literature and examination of specimens in the local collections yielded clues which might be construed as indicating that hybridization was taking place in nature, but no concrete evidence was uncovered. A five year study of this genus both in the laboratory and in the field has disclosed facts which may be of considerable importance in moulding our concepts of the much debated "Species Problem."

B. RESUMÉ OF THE PREVIOUS WORK ON LEPIDOPTERA HYBRIDS

A very considerable amount of work has been done on hybridization in the Lepidoptera covering a period of more than fifty years. It can be grouped conveniently into three classes: first, the pioneer work of Standfuss and his colleagues on hybridization in the genus *Saturnia*; second, the very extensive work with the Sphingidae of Europe and to a lesser extent of America; and third, the work of Harrison and his colleagues with the Bistoninae and of Pictet with the races of butterflies and moths in the Swiss Alps.

THE WORK OF STANDFUSS

Dr. Standfuss of Vienna crossed the various species of the Palearctic genus *Saturnia* and obtained a low percentage of matings (they

do not cross in nature) and even smaller percentages of fertile eggs and of imagoes. A large number of his hybrid broods were composed of only one sex. His general conclusions may be summarized as follows. (1) The offspring tend to resemble the phylogenetically older parent in morphological and physiological characters. (2) There appears to be a certain predominance of characters inherited from the male. (3) The females are sterile and the males more or less fertile. (4) The individuals of the second generation are very variable, tend to approach the phylogenetically older parent, and include a considerable percentage of gynandromorphs.

THE WORK WITH THE SPHINGID HYBRIDS.

The principal workers with the Sphingid hybrids were Denso, Standfuss, Lenz, Kysela, Dannenburg, and Rebel. The crosses were made between the various species of the genera *Celerio*, *Smerinthus*, *Mimas* and *Chærocampa*. Practically all possible combinations within the various genera were obtained and many intergeneric crosses made. Among these were a number of interfaunal crosses such as those involving *Smerinthus ocellata* or *Amorpha populi* of Europe as one parent and *Smerinthus jamaicensis*, *S. cerysii*, *Paonias myops* or *P. astylus* of North America as the other. Secondary and tertiary hybrids in all combinations were produced in many cases, particularly using the species *Celerio galli* and *Celerio euphorbiæ*. The principal contributions to the knowledge of hybrids made by this group of investigators were the production of intergeneric hybrids and the filling in of the gaps in the knowledge of the types of hybrids.

THE WORK OF HARRISON AND HIS COLLEAGUES

Harrison has attacked the problem of hybridization principally from the angle of phylogeny. By means of his experiments on the Bistoninæ he was able to demonstrate that the fertility of the hybrid is a function of the specific divergence between the parents. It was also demonstrated that the phenomena of dominance in the hybrid depends on this same factor, being not evident when there is considerable divergence. Harrison correlated the data from geographic distribution with that obtained from hybridization to formulate the relationships and probable origin of the species in the genera *Lycia*, *Pæcelopsis* and *Nyssia*. Perhaps the most important contribution of Harrison and his co-worker, Doncaster, was the finding of an irregular

chromosome behavior in the hybrids. This provides a possible explanation for the infertility of some, for the gynandromorphism and for the queer sex ratios often obtained.

THE CLASSIFICATION OF HYBRIDS

As a result of these various experiments with hybrids of the Lepidoptera, a classification of hybrids was proposed by Ræpke. This classification, reported by Morgan in the American Naturalist, Volume XLIII, is reproduced here with an additional class added to each end.

0. Those hybrids which, although they undergo considerable embryonic differentiation, fail to hatch, or hatching, fail to complete the larval development, because of disharmony of parts.

1. "First, those hybrids that are so abnormal (atypic or sexless) that their sex cannot be determined.

2. "Second, those hybrids in which only one sex develops, generally the male; females also rarely appear, but are so imperfect that reproduction is impossible. The males also are sterile.

3. "Third, those hybrids in which both sexes appear in normal proportions; the females sterile, the males crossed back to the parent species fertile in various degrees. The offspring of such a union are, however, very abnormal and monstrous both in their primary and secondary sexual organs. In certain series gynandromorphs appear in surprisingly large numbers.

4. "Fourth, those hybrids in which the females although appearing normal lay either no eggs or abnormal eggs. The males are like those of the last category or like those in the next.

5. "Fifth, those hybrids in which the females produce only embryos, or if the caterpillar stage is reached at all, the young are weak. When it has been possible to rear moths by back crossing these females to the parent species (or from male hybrids of the same cross) only males develop but in such scanty numbers that they have not been tested further."

To this we might add another class.

6. Those hybrids in which the fertility of both sexes approaches that of the parent species in that secondary, tertiary, or other hybrids can be obtained. Example: *Celerio galli* x *Celerio euphorbiæ*.

It may be further stated that these classes, while they show the manner in which the hybrids grade from one extreme to the other in

viability and reproductivity, are artificial groupings of a more or less uniform gradation.

THE WORK OF PICTET

The work of Pictet in his analysis of the Lepidopterous fauna of the Swiss National Park, while not directly involving species-hybridization is important in that he was able to show in a number of cases that intermediate forms found on the barrier between two subspecies could be duplicated by hybrid forms produced in the laboratory. He appears to be the first to demonstrate by synthesis the possible hybrid nature of an intergrade.

THE BEARING OF ALL THESE ON THE PRESENT PROBLEM

From the above incomplete and much abbreviated account of the previous work on hybridization, it is hoped that the reader may have gleaned an understanding of the phenomena as they are manifested in the Lepidoptera. The experiments described in the following pages partake of the nature of all of those listed above, in that the relationships between the various species and forms in the genus are determined from the data obtained through hybridization as well as from distribution and comparative morphology, as in Harrison's work; while the hybrid nature of certain intergrading forms is demonstrated through synthesis in much the same way that Pictet analyzed his intermediate forms in the Swiss Alps.

C. PRECEDING WORK WITH THE GENUS *PLATYSAMIA*

The various species and forms of the genus *Platysamia* have been crossmated and the hybrids reared to the imago many times as recorded in the literature. Every sizable collection in North America contains one or more of these hybrids. As yet no secondary hybrids have been reported. For a number of years after the publication of the description of *Platysamia columbia* (Smith) = *Samia columbia* (Smith), a controversy raged as to whether or not it was of hybrid origin. Dr. H. A. Hagen of Cambridge, Massachusetts, suggested that it might be a hybrid, possibly between *P. cecropia* (L) and *Callosamia promethea* (Drury).¹ This was soon disproven. Most of the published records of hybridization in this genus are mere isolated notes to the effect that a hybrid had been more or less ac-

¹Hagen, H. A. "On *Attacus* (Samia) *Columbia* and its Parasites." *Bulletin of the Buffalo Society of Natural Science*, Jan. 1875.

cidentally obtained. To my knowledge, the only careful study was made by Miss E. L. Morton of Newburg, New York.² She had *P. cecropia* and *P. gloveri* emerge and mate in the same cage. The hybrids from this and from other crosses were reared to the imago stage and all were reported to be completely sterile. The best summary of the early studies in this genus was made by Tutt in the third volume of his work "A Natural History of British Lepidoptera" in which he assigned names to Miss Morton's hybrids and to those produced by Heyer.³ The names which are not recognized under the International code were *P. griffithsi* (Tutt) = *P. cecropia* ♂ x *P. gloveri* ♀; *P. watsoni* (Tutt) = *P. cecropia* ♂ x *P. euryalis* ♀; *P. americana* (Tutt) = *P. columbia* ♂ x *P. cecropia* ♀; and *P. heyeri* (Tutt) = *P. euryalis* ♂ x *P. cecropia* ♀.

II. MATERIAL

A. THE GENUS PLATYSAMIA

The forms of insects herein discussed are referable to the scaly winged order Lepidoptera. Since they have bipectinate antennæ they belong to the suborder Heterocera, the moths. The hind wings have the most posterior vein (3rd Anal or lc) absent and the most anterior one (Sc-R₁ or 8) diverging from the cell at the base. The fore wings have vein M₂ or 5 arising from above the middle of the discocellular vein. In addition, they contain "no sensory organs of radiating bristles behind the antennæ, no tympanal cavity at the base of the abdomen, no proboscis, no tooth on tarsal claw, and the frenulum is completely absent,"⁴ placing them in the family Saturniidae. In the most recent check list of the North American Saturniidae⁵ they are placed in the genus *Platysamia*.⁶

The species of the genus *Platysamia* are characterized by having

²Morton, E. L. "Hybrid Saturniid Moths and their Larvæ." *Proceedings of The Entomological Society of London*, 1895, pp. 34-35.

³Tutt, J. W. *A Natural History of British Lepidoptera*, London, Vol. 3, pp. 292-293.

⁴Jordan, K. "Note on the families of moths in which M₂ (vein 5) of the fore wing arises from near the center or above the center of the cell." *Novitates Zoologica*, Vol. 30, 1923, pp. 163-166.

⁵Barnes, W. and Benjamin, F. H. "Check List of the Lepidoptera of Boreal America, Superfamilies Sphingoidea, Saturnoidea and Bombycoidea of the Families Syntomidae and Arctiidae." *Pan. Pacific Entomologist*, Vol. 4, pp. 87-89, 1927.

⁶See Appendix I.

bipectinate antennæ, the pectinations of the male being much longer than those of the female; heavy furry bodies; and large broad wings. The markings common to all of the species consist of a basal and an extradiscal white cross band and a curved discal spot on both wings and an apical ocellus on the forewing. The eggs are ovate, white, covered with a gummy brown cementing material and are laid in groups of from three to six. The larvæ are cylindrical and equipped with eight rows of warty tubercles armed with spines. The first segment has six, segments two to five have eight, segments six to ten have six, segment eleven has only five because of the fusion of the tubercles representing the two dorsal rows, and segment twelve has only four. In the last instar the dorsal tubercles of segments two, three, four and eleven are large and swollen. The cocoon is densely woven, composed of an inner and an outer shell, is open at one end, and is rigidly attached to some support, usually a branch of the food plant.

The first to be described, of the species concerned in this report, was *Phalæna cecropia* (Linnaeus) 1758. Hübner placed it in his generic subdivision *Samia*⁷ along with *cynthia* (Drury) and *promethea* (Drury) in 1816. In 1855 Walker redescribed the genus *Samia*⁸ and dropped *cynthia* (Drury) from the list of its species. In 1865 Grote fixed *cynthia* (Drury) as the type of *Samia*, confirmed *promethea* (Drury) as the type of Packard's genus *Callosamia*⁹ and named *cecropia* (L.) as the type of his new genus *Platysamia*.¹⁰ The species *cecropia* (L.) and its relatives were referred to a variety of genera in the succeeding years including *Attacus*, *Bombyx*, *Hyalophora*, *Samia* and *Platysamia*. On the whole, *Platysamia* predominated until about 1900. This name was then replaced by *Samia*. The most recent check list, that of Barnes and Benjamin, reestablishes the name *Platysamia*.

The forms included in the genus are:

Platysamia

1. *cecropia* Linn.
2. *columbia* Smith.
 nokomis Brodie.
 winonah Brodie.
3. *gloveri* Strecker.
4. *euryalis* Boisduval = *ceanothi* Behr = *californica* Grote = *rubra* N. & D.
 kasloensis Cockerell.
 cedrosensis Cockerell.

⁷⁻¹⁰See Appendix I.

B. DESCRIPTIONS AND DISTRIBUTIONS OF THE FORMS

In the following descriptions no differentiation will be made between species, forms, etc., because the writer is not in accordance with the accepted status of the organisms. Their relationships and taxonomy will be discussed later.

Platysamia cecropia (Linnæus)

Original description in *Systema naturæ*, Tome I, Carl Linnæi, 1758.

Cecropia

3. *P. Bombyx elinguis, alis patulis subfalcatis griseis: fascia fulva, superioribus ocello subfenestrato ferrugineo.* M.L.U.

Catesb. car. 2. p. 86. t. 86.

Habitat in America septentrionali.

Supplementary Description: Head, thorax and abdomen brick red, tegula white, abdomen with white and black intersegmental bands, spiracles red, ringed with white.

Ground-color of wings black suffused with white or yellow scales giving it a grizzled appearance. Fore wings with basal area red; basal line white, edged externally with black. Medial area usually suffused with red, densely along the basal line and fading out distally. The extradiscal line is white, edged outwardly with red. It may be straight, angled, curved or scalloped, but always tapers towards the costal margin of the wing, sometimes not reaching the costa. The extradiscal line is bordered distally by a band of the ground color which reaches to the ocellus and bears irregular black blotches between the veins at its outer edge. There is a fine brownish gray subterminal line much indented between the veins. This line is separated from the band of ground color by a yellowish gray area and from the terminal line by a pale cream area. The terminal line is narrow, uniform in width and pale brown in color. The ocellus, located in cell R_5 (or II_2) is oval, black with a blue crescent whose horns point towards the outer margin. A narrow red bar extends distally from the anterior edge of the ocellus parallel to the veins. A zigzag white line extends from the ocellus to the costa and is bordered proximally by a patch of lavender scales and distally by a red spot near the costa. The discal spot which is shaped like an inverted comma with the narrow end directed outwards parallel to the costa, varies greatly in size. It is brick red, bordered with a narrow black line and usually has a white center.

The hind wing is marked much like the front wing with the following exceptions. The area between the costa and subcosta is yellowish white. The red basal area is obsolete, the white basal band extending to the wing base. The extradiscal line is wider, particularly the red component, and does not taper. There is an additional pale scalloped line which separates off small spots from the outer edge of the band of ground color that is distal to the extradiscal line. There is no ocellus. The discal spot is comma shaped with the point extending outwardly between veins m_2 and m_3 but never reaching the extradiscal line. It is brick red with a fine black border and a white center.

The undersides of both wings have the basal white band and the red suffusion missing. Aside from this and the addition of a general suffusion of white or yellow scales, the markings of the upper side are reproduced below.

Variation: The ground color may vary from deep black to pale speckled gray. The amount of red suffusion in the medial area may vary from none, as in some eastern specimens, to almost entire red, as in specimens from North Dakota. The white part of the extradiscal line may be lost on the front wing and reduced to the width of a hair on the hind wing. The red band may be reduced to a few scales or, rarely, entirely lost. The discal spots vary greatly in size but always retain their characteristic comma shape.

Larva: The larvæ are black marked with yellow in the first instar, yellow marked with black and with black tubercles in the second, yellow or green in the third, and pea-green in the remaining instars. In the third, fourth and fifth instars the side tubercles are blue or blue tipped with white. In the third and fourth stages the dorsal tubercles on segments two and three are bright cherry red while the remainder are straw yellow. In the last instar (fifth) all of the dorsal tubercles may be pale yellow, but usually those on segments two and three are bright red while the others are pale yellow. Very rarely, the dorsal tubercles may be a burnt orange on segments two and three, smoky yellow on segments four and eleven and pale yellow on the others. The shade of each dorsal tubercle varies from time to time in the same instar but the fundamental color remains the same. The amount of heavy black chitin on the tubercle also varies. All of the species and hybrids of this genus that have been reared by the writer have shown this variability in these two respects. The full

grown larva of *Platysamia cecropia* attains a length of from four to six inches and may be as thick as a man's thumb.

Cocoon: The inner and outer cocoons are loosely connected. The inner cocoon is a long ellipsoid with the head end closed as with a draw string, while the outer may be one of two forms: either closely applied to but easily separated from the inner, or a loose envelope many times the size of the inner cocoon. The outer cocoon is usually pointed at both ends and attached throughout its length. Both cocoons are a light tawny color.

Food Plants: The larvæ of *P. cecropia* may feed on almost any deciduous tree or shrub and even occasionally on the broad leafed evergreens, but the preferred hosts are the elderberry (*Sambucus*), maple (*Acer*), willow (*Salix*) and the wild cherries (*Prunus*).

Distribution: *Platysamia cecropia* is found throughout the eastern states from Maine to Florida and westward into the foothills of the Rocky Mountains. In Canada, it occupies the Maritime Provinces and extends an undetermined distance north into Quebec. Its northern limit in Ontario appears to be a short distance south of Cochrane in the east and the Lake of the Woods district in the west. In Manitoba the species is not found a dozen miles east of Winnipeg, but the vanguard has pushed northward along the Red River to Lake Winnipeg, perhaps farther, and west of Winnipeg extends only to the Assiniboine River. While its western limit in general is the Rocky Mountains, if the records of capture are accurate, *P. cecropia* has replaced *P. gloveri* in eastern Montana within the past fifty years, has become plentiful in southern Alberta within the past few years and has invaded the Black Hills within the past decade. Cockerell reported that *P. cecropia* had invaded the territory of *P. gloveri* at Boulder, Colorado in 1929. The species is found in eastern and southern Texas and there is a specimen in the United States National Museum from Jalapa, Mexico. There appears to be a wave of *P. cecropia* in numbers sufficient to completely defoliate trees pushing across the northwestern part of its range. Whether this represents a new invasion made possible by the tree planting activities of the settlers, or to a temporary lack of parasite and disease control, there is no way of determining.

Diagnostic characters: The grizzled ground color and tapering extradiscal band on the fore wing and to a certain extent, the red part of the extradiscal band will separate this species from all the others

in the genus. The larva may be distinguished in the third and fourth and usually the fifth instars by the fact that the dorsal tubercles on segments two and three are red while the remainder are yellow. The cocoon may be recognized by its tawny color, its long line of attachment and the fact that it is pointed at both ends.

***Platysamia gloveri* (Strecker)**

Original Description: *P. gloveri* was described by Herman Strecker in his "Lepidoptera Rophaloceres and Heteroceres" in 1872.

"*Platysamia gloveri*: *Male*. Expanse, four and one-half inches.

"*Antennæ* pectinated. Head and thorax dark brownish red; collar white; abdomen alternately banded with dark brown and white.

"Upper surface, primaries, inner half dark reddish brown, with a dirty white band near the base and a small white oval spot bordered on the outer and inner sides with black; the dark red colored space is bounded outwardly by a white transverse band extending from the costa to the inner margin, widening at the latter termination; the space immediately beyond the white band occupying fully two-thirds of the exterior half of the surface, is dark gray, composed of black and white scales, the exterior portion being the darkest; the remaining space between this and the exterior margin is dirty gray, transversed by a serpentine black line; a short space in from the apex on the costa is a small black spot, from which a zigzag white line extends a short distance to another larger black spot of an oval shape, which has within it a pale blue crescent; the space from this latter black spot to the costa, and from the zigzag line almost to the white transverse band is violet.

"Secondaries have a white basal patch, also a white transverse band as in *Cecropia*; the color between this band and the base is dark brownish red; in the center is a moderately large lunate discal spot, white edged with black; of the remaining space, between the transverse band and the exterior margin, the inner two-thirds is composed of black and white scales, as in the primaries, and the outer third is light, dirty gray, which latter is divided by a black line, on the inside of which line, running parallel with it, is a row of irregularly shaped black spots.

"Under surface same as above, with the exception of the ground color of the secondaries between the transverse bands and the base which is composed of black and white scales instead of being dark red as on the upper surface.

"*Female*. Expanse, five and one-quarter inches.

"*Antennæ* not as broadly pectinated as in the male. Head and thorax brownish or brick red, much the same as in ordinary forms of *Cecropia*; abdomen alternately banded with the same color and white.

"On the primaries the transverse white band is somewhat irregular and rounded outwardly; the basal band also rounded; the discal spot larger than in male, and slightly lunate; the ground color between the transverse band and the base is brownish red, of a slightly different tint than the thorax; the portion beyond the transverse band, light dirty gray as far as the serpentine line, the inner third of it powdered with a band of reddish scales, broader near the exterior margin, and narrowing towards the costa; margin outside of the serpentine line dirty white, shaded slightly exteriorly; the black apical spots and violet patch same as in male.

"Secondaries. Color same as in primaries; ornamentation same as in male, except the discal spot which is double the size.

"Undersurface marked same as the upper; coloration same as in underside of male.

"Habitat: Arizona."¹¹

¹¹Dr. Strecker stated further that he had received "examples of it, which were said to come from lower California, but as *L. weidermeyerii*, *Parn. smintheus*, and other northern montane species were sent in company with it, I expressed my doubts regarding that locality, which have since been confirmed by my receiving a female from Arizona." Present knowledge of the distribution of the *Platysamia* indicates that the specimen figured could not possibly have come from Lower California.

With the assistance of Mr. Benjamin, the writer had the pleasure of tracing the history of Strecker's specimens at the United States National Museum. The specimens in question (six) were received by Dr. Glover from a Dr. Edw. Smart along with several *Nemophila*, a *Syneda* and the specimens listed by Strecker. This happened before the establishment of the National Museum and so the letter accompanying the donation has not been found. Dr. Glover recorded the specimens as having come from "South Calif." and made copper plate etchings of all of the species. The plates were subsequently destroyed and never published, but manuscript copies are deposited in the National Museum library.

The specimens accompanying the *gloveri*, particularly the *Basolarchia weidermeyerii*, as delineated in the plates could only have come from the Rocky Mountain region or from a colony of Rocky Mountain fauna in California. Such a colony is not known to exist.

On searching through the files of the National Museum, a donation of a portion of a fossil swan by a Dr. Edw. Smart of Hastings, Nebraska was found recorded. In his letter, Dr. Smart stated that he had dug up the specimen from an Indian mound in 1875. This would place him east of the Rockies about the time that the *gloveri* were taken. In the handwriting of the letter, there appears to be little difference between the o's and the a's.

It is quite possible that the donations of Lepidoptera and of the fossil swan came from the same man, and that Dr. Glover mistook the longhand "South Col." to be "South Cal.". This would make the type locality of the male figured and described by Strecker to be South Colorado and this fits perfectly with subsequent material from that district.

Variation: In the central part of its range, in Colorado and Utah, the ground color of *P. gloveri* is wine red. The discal spots are uniformly reniform, without any appreciable point and vary greatly in size. Also there are no red scales bordering the extradiscal line distally although there is an occasional purplish tinge to the gray subterminal area. Neumægon described a form, *P. gloveri reducta*, from Gibson Gulch, Colorado at an altitude of 11,000 feet that is characterized by having only about half of the expanse of the normal form and by having the gray subterminal band greatly widened at the expense of the central red ground color, the gray band occupying the entire terminal half of the wing. In Montana, Wyoming, South Dakota (Black Hills) and in Alberta the moths approach the form *reducta* in size, but have the normal *gloveri* markings, although one specimen from Alberta has the markings as in *reducta*. The size is apparently a function of the severity of the climate. At the southernmost known limit of the range, in Pima County, Arizona, the characters by which the female type specimen differs from the male type specimen are accentuated. Thus, the discal spots have a long point extending distally from the anterior end and sometimes reaching almost to the extradiscal line. The extradiscal line is edged outwardly with pink scales. The gray subterminal band is more or less suffused with rusty brown.

Larva: The larvæ resemble those of *P. cecropia* with the following exceptions. The green color usually has a bluish tinge. In the third and fourth instars the dorsal tubercles are either all red or all yellow, but *all* the same shade. In the third instar, there is a considerable development of the black chitin which partially obscures the red in some specimens or may even completely cover it. In the last instar the dorsal tubercles are all straw yellow, but in a few exceptions, those on segments two, three and four are slightly deeper in shade. The only Montana specimen that I have seen had the dorsal tubercles of segments two and three a dull burnt orange, those on segment four a dirty yellow while the remainder were pale yellow, but this specimen was taken when full grown in Glacier Park on the edge of the zone of intergradation with *P. euryalis* and is probably not pure *P. gloveri*.

Cocoon: The cocoons are small in proportion to the moth that emerges from them, and have the diameter larger in comparison with the length than in *P. cecropia*. They are pointed only at the open end

and are attached for less than half their length. The inner and outer shells are so closely woven together that they can scarcely be separated. The silk is white when woven and the outside of the cocoon is covered with ridges. When the spinning is finished, the silk is impregnated with a fluid that forms a blackish gum that does not reach the ridges which remain silvery against a dark background.

Food Plants: In Utah *P. gloveri* feeds on the sand-bar willow (*Salix*) and on the wild currant (*Ribes*). In Montana it feeds on the wild currant and on alder (*Alnus*). Perhaps there are other hosts.

Distribution: *Platysamia gloveri* is found throughout the Rocky Mountain region in the United States and its range probably extends southward into Mexico. It extends westward to the deserts of the Great Basin and in Montana to a line a few miles west of the Continental Divide. A specimen was taken in the Black Hills of South Dakota in 1933 and the species was once found as far east as Miles City in Montana but is no longer to be found east of the mountains. In Alberta it tends to intergrade with the form *P. nokomis* from which it can scarcely be distinguished.

***Platysamia columbia* (Smith)**

Original Description: Proceedings of the Boston Society of Natural History, Vol. 9, December 2, 1863, by S. I. Smith, read by Mr. A. E. Verrill. Printed in 1865.

"Description of a species of *Samia* supposed to be new, from Norway, Maine.

Samia Columbia

"*Male*—Antennæ black and broadly pectinated. Palpi dark maroon brown. Thorax with a white band before; upper side dark maroon, with a short grey band behind; beneath black, the legs also black, slightly tinged with brownish towards the extremities. Abdomen annulated with alternate black and dirty white.

"Above. Primaries with a greyish white band near the base, extending from the inner nearly to the costal border, and enclosing a reddish brown patch at the base. The middle area of the wing is dark brown, tinged with reddish towards the center, and contains a triangular white discal spot; bordered on the side towards the base with black, and on the other sides with greyish brown. There is a narrow white transverse band, wider towards the inner border, between the middle and the outer area. A sinuous black line on a grey colored ground, crosses the posterior border. Near the apex there

is a round black spot, containing a bluish white crescent, with its horns toward the outer border; between this and another small oblong black spot at the apex there is a zigzag white line in the form of a W, with the upper side toward the outer border. A space along the costal border, extending from this zigzag line almost to the middle area is bluish white, growing darker and more indistinct as it approaches the transverse band. A short band between the middle area and the greyish outer border, extending from the inner border a third of the way across the wing is dark greyish brown becoming lighter as it leaves the inner border.

"Secondaries with a small dirty white spot on the shoulder and the anterior border just edged with the same. A white transverse band similar to the one on the primaries. The space between this band and the base of the wing is dark brown, with the discal spot large and white. The outer border is margined with clay color, bounded on the inside with an arcuate black line. Just inside of this line there is a band of black spots on a greyish ground; the space between this band of spots and the transverse band is occupied by a wide greyish brown band.

"Beneath, the markings of the upper side are repeated; but all the reddish tints are wanting, so as to leave the ground color of the wings black, intermingled with whitish scales. The discal spots are bordered with black.

"*Female*. The antennæ are less broadly pectinated than in the male and all the colors less intense. Discal spots on the primaries almost obsolete; being only short lines bordered with black, and parallel to the transverse band. Discal spots of the secondaries much smaller than in the male and more rounded.

"Expanse of wings: ♂ 4"; ♀ 4.9" 1 ♂ 1 ♀."

Variation: The discal spots of the hind wings may be oval, or reniform with the upper end drawn out into a slight point. Out of 57 specimens in the writer's collection, eight in the Redpath Museum at Montreal, four in the Museum of Comparative Zoology at Cambridge, three in the Carnegie Museum at Pittsburgh, and 23 in the United States National Museum, 95 specimens in all, 42 have red along the outer margin of the extradiscal band varying from a thin line of scales visible only on the underside to a well defined band wider than the red band of some *P. cecropia*.

Larva: The larvæ of *P. columbia* are characterized by the great development of the heavily chitinated patches on the tubercles with the result that these tubercles are more slender than those of the other forms and the color is usually hidden. The dorsal tubercles of the third and fourth instars, when they show any color, resemble those of *P. cecropia* except that those of the fourth segment are a reddish

orange instead of yellow. Also in the last instar, this set of tubercles is the same shade of red as those on the second and third segments while the remainder are yellow with a pink tinge. The larvæ of *P. columbia* are smaller in all stages than those of *P. cecropia* or *P. gloveri*.

Cocoon: The cocoon resembles that of *P. gloveri* in structure and color but is slightly darker, smaller and more slender. The puckered opening, however, is about the same size as that of *P. gloveri*, making it much more conspicuous on the small cocoon.

Distribution: According to records from before 1900, *P. columbia* extended from western Ontario to Maine and down into southern Michigan. At the present time, it is limited to the swampy region east of Winnipeg, along the northern shore of Lake Superior and east to the region of North Bay, Ontario. A small colony of the species still remains in Michigan and it has been recently reported again from Maine. No specimens are recorded as taken in southern or eastern Ontario or in Quebec for thirty years. The principal cause for the restriction of range in Canada appears to have been the almost complete destruction of the larch (*Larix americana*), the food plant of *P. columbia*, by the larch sawfly although disease may have been an equally important factor.

***Platysamia nokomis* (Brodie).**

Original Description: The form *nokomis* was first described by Mr. William Brodie in a paper read before the Natural History Society of Toronto. The paper was not published, and both it and the types of *P. nokomis* and *P. winonah* were lost. Later Mr. Brodie redescribed the forms in the *Biological Review of Ontario*, 1894. The type locality is listed as Carberry, Manitoba. The description follows:

"The following points of difference may be noted between the *columbia nokomis* form and the *columbia* form, as represented by Ontario specimens, and as compared with Smith's description of *columbia*, parts of which are given in brackets. The standard of colors is Ridgeway's *Nomenclature of Colors*.

"Antennæ, central shaft, bright reddish brown; pectinations darker [black]; palpi, light liver brown [dark maroon brown]; dorsum of thorax, bright reddish liver brown with a posterior pure white band [dark maroon with a short grey band]; underside of thorax reddish liver brown [black]; legs, reddish brown, pile darker [black, slightly tinged with brownish]; abdomen with alternate annulations, bright liver brown and pure white [black and dirty white].

"Primaries above with a rather sharply elbowed pure white line [greyish white]; the middle area of the wing is bright reddish liver brown [dark brown], and contains a central ovate white spot [triangular]; this bright area is separated from the costa by a moderately wide longitudinal greyish stripe. Secondaries with a large white spot at the shoulder [small dirty white]; the central area, bright reddish liver brown [dark brown], having a central white spot, which varies from kidney form to curved pear form and varying much in size, but always larger than the corresponding spot on the primaries; but no sexual difference could be observed either in the size or in the form of these central spots.

"The primaries beneath have the space from the shoulder to the median white crossband of a maroon brown [black], and generally the underside of the wings of *columbia nokomis* is brighter colored than that of *columbia*."

Supplementary Description: The collar is white and the discal spots (Brodie's central white spots) are bordered with tan and outwardly ringed more or less completely with black.

Variation: On the whole there is a tendency for the reddish portions to be brighter than the "reddish liver brown" of Brodie's description, usually as bright as the claret of *P. gloveri* or even brighter. In three out of six specimens at the U. S. National Museum, in 15 out of 21 specimens in the writer's collection and in about half of a considerable number of specimens noted in the collection of Manitoba entomologists there is a red band along the distal border of the extradiscal white crossband ranging from a few scattered scales to a solid band equal in width to the white band.

Distinguishing Characters: *Platysamia nokomis* can be separated from its eastern neighbor, *columbia*, much more easily than from its western neighbor, *gloveri*. From the former it may be distinguished by its lack of melanic suffusion, its wider extradiscal band and its wider ovate discal spots. While an experienced lepidopterist can separate most of the *nokomis* from *gloveri*, there is no single constant character or combination of characters that can be listed as diagnostic of the "species." This opinion is based on examination of more than a hundred of each "species" collected over almost their entire ranges.

Larva: The larvæ of *Platysamia nokomis* differ structurally from those of *P. columbia* in that they lack the heavy black chitization of the tubercles in the third and fourth stages, resembling those of *P. gloveri* or *P. cecropia* in this respect. The first instar is black showing yellow spots when full fed. The second is a brilliant orange-

yellow fading to a pale canary; the tubercles are black. The third instar is a pale pea green with canary yellow at the base of all the dorsal tubercles except the first. The fourth instar is bluish green, the dorsal tubercles from segments two to eleven all bright yellow, the side tubercles blue. The fifth stage is a greenish slate color as in *P. gloveri*, the dorsal tubercles all being ochre yellow, those on segments two, three and four having a patch of heavy black chitin on the side towards the head.

Cocoon: The cocoon resembles that of *P. gloveri* except that it is smaller and more silvery. It is slightly larger than that of *P. columbia* and is less slender.

Food Plants: The principal food plant of *P. nokomis* is the wolf willow (*Elæagnus*). It also feeds to a certain extent on the willow (*Salix*).

Distribution: *P. nokomis* is found in Manitoba west of Winnipeg and north of the Assiniboine River. It is also found in Saskatchewan and Alberta, although many, if not all, of the specimens from the latter province may be *P. gloveri*.

Platysamia winonah (Brodie)

Original description: *Platysamia winonah* was described by Mr. William Brodie along with *P. nokomis*. In his redescription of the latter he makes the following comment:

"Early in 1883 I received a package of cocoons of *P. columbia* and *T. polyphemus* collected by W. G. A. Brodie near Pelley, N.W.T. Only one imago emerged from this lot, from a *P. columbia* cocoon, and it differed so very much from the Manitoba form that I considered it a well marked variety, being much less in size and of much brighter colors, and the boundaries of the colors much more distinct for the Pelley form [I proposed the name] *P. columbia winonah*. . . ."

"As I have not seen but one specimen of the *columbia winonah* type, little need be said about it. My specimen may have been representative of an extreme northern group, or it may have been only a strongly marked specimen of *columbia nokomis*."

This is all that is known of *P. winonah*, and until more specimens are collected at or near the type locality, the writer is unable to comment further regarding the exact status of the organism represented by the name.

Platysamia euryalis (Boisduval)

This species of *Platysamia* from California was first described and named by Boisduval in 1855. A month later Behr described it in California, but applied no name and a descriptive adjective used has crept into use as a name. A little later in the same year the name *ceanothi* was indirectly attributed to Behr when specimens donated by him were recorded under that name. Grote, refusing to recognize Boisduval's description, again described it in 1865, applying the name *californica*.

Original Description: Boisduval in "Bulletin Entomologique," 1^{er} trimestre, 1855, Societe Entomologique de France.

"Tels sont entre autres la *Saturnia euryalis*, voisins de la *cecropia*, de l'Amerique du nord, mais beaucoup plus petite et fort distincte au premier coup d'œil, par la longue lunules des ailes inferieures qui traverse la bande mediane; . . ."

Grote's description ¹² is somewhat more complete and will serve much better than a supplementary description by the writer.

"*Platysamia californica*"

"Male and Female—smaller than *P. cecropia*. Primaries reddish-brown shaded subterminally with a brighter plum-colored tinge, *with no gray scales whatever*. [Italics mine] A broad basal white arcuate band, running from the interior margin, at extreme base, to just below the costa at basal fourth, narrowly lined outwardly with dark scales. Beyond the disc a moderate, whitish, sub-luniform spot, shaded with buff. A nearly straight sub-terminal whitish band narrower than the basal band, lined outwardly with dark scales. Subterminal space with a brighter, somewhat peach-colored shade, which becomes less distinct outwardly. As in *P. cecropia*, the apical interspace has a W-shaped pale mark preceded by lilac scales. Below, in the post apical interspace, is a black ocellus, margined with a blue annulus, obsolete outwardly. Terminal space dull pale wood-color, much the same shade as in *P. cecropia*, but narrower. The terminal line is narrow and but slightly waved.

"Secondaries resemble primaries in coloration. A few whitish scales at extreme base. A larger, similarly colored sub-luniform spot to that of the primaries, which is produced so as nearly to attain to the outer transverse white band, which latter matches that on the anterior wings. Under surface darker, but resembling upper surface

¹²Augustus R. Grote. "Notes on the Bombycene Moths of Cuba." *Proceedings of the Entomological Society of Philadelphia*, Vol. 5, p. 229, 1865. (The reference is to the footnote.)

in ornamentation; secondaries with a white patch at base on costa."

"Head, capital appendages, thorax and abdomen reddish-brown very nearly concolorous with the wing. 'Collar' entirely white. Abdomen with long white hair fringing the segments posteriorly, very distinct in female; in the male, bands are more confused. The sexes resemble each other.

	♂	♀
"Expanse	3.85 in.	4.25 in.
Length of body	1.10 in.	1.85 in.
Habitat: California (San Francisco)"		

Variation: The length of the discoidal lunules varies greatly; the point often penetrates and extends beyond the extradiscal line. The extradiscal line on specimens from high altitudes is usually bordered on both sides with dark scales while that of lowland specimens is not. Many of the Oregon specimens are darker than those of California.

Larva: The writer has never reared pure *P. euryalis* and the published notes describing the larval stages do not check with data obtained from hybrids. The first stage is black, becoming spotted with beeswax yellow when full fed. The second instar is straw yellow with black tubercles. In the third instar, the body is green, the dorsal tubercles are concolorous, and yellow, salmon or red, while the side tubercles are turquoise blue. In the fourth and fifth instars the body is pea green and the dorsal tubercles, as far as known, are concolorous and straw yellow. The side tubercles are blue or blue tipped with white.

Cocoon: The cocoon of *P. euryalis* is a tawny brown color as in *P. cecropia* and lacks the dark gummy impregnation found in *P. gloveri*. It is flask shaped, the main body being ovoid, almost round, with a slender neck at the open end. It is seldom fastened longitudinally to a support as are the cocoons of the other members of the *Platysamia*.

Distribution: This species is found throughout California, western Nevada, Oregon and Washington to Vancouver Island, British Columbia. In eastern Washington, in Idaho and in British Columbia it intergrades with *P. gloveri*, the mid-intergrade having been assigned the varietal name, *kasloensis*, by Cockerell.

***Platysamia kasloensis* (Cockerell)**

Original Description: The following description appears as a footnote in Part III, page 226, of Packard's "Monograph of the Bombycene Moths of North America," the third part of which was edited by Dr. T. D. A. Cockerell after Dr. Packard's death.

"*S. rubra kasloensis*, collected by Dr. H. G. Dyar at Kaslo. This

is the form described by Mr. Cockle. . . . It is a submelanic race, darker above than the typical; much blacker and less red below."

Mr. Cockle's description follows. (It was never intended as a scientific description and is consequently rambling. Only the descriptive portions are quoted.)

"There is undoubtedly a local race of the species [rubra = euryalis] to be found in the interior of British Columbia, the general color of which is purplish-brown above on all wings, whilst the underside is always greyish. . . . The markings of both forms [rubra and the British Columbia form] are very variable, the only difference being in the submarginal line which, instead of being deeply dentate as in the California species, has a tendency to lose this dentation, the line being a series of loops bent outwardly with, in some cases, a slight dentation between the veins."

Mr. Cockle continues with the following comment which will be referred to later:

"I have frequently been met with remarks from collectors to whom I have sent this form of rubra that *it was nearer to gloveri than to rubra*, [Italics mine] but the two species are sufficiently distinct in the median lines to prevent all possibility of mistake, but at the same time the northern form of rubra is so different in appearance to warrant a separation and possibly, when the investigation is carried to completion, even a new name."¹³

It may be said in passing that judging from about two hundred specimens of the forms involved, either specimens in the writer's collection or photographs of specimens in other collections, the shapes of the submarginal and median lines upon which Mr. Cockle effects his separation are not valid characters but subject to great variation in all of the species.

Supplementary Description: The general tone of the ground color may vary from red as bright as that of *P. euryalis* to a deep reddish brown. The discoidal lunules may vary from comma-shaped spots reaching to the extradiscal line on the hind wing to spots that are almost obsolete. All of the specimens have a mixture of red and grey scales in the band of ground color just outside the extradiscal line. This last character may be considered as diagnostic of the form.

Larva and Cocoon: The writer has never seen either larva or cocoon, all of his specimens having been taken on the wing, but the hybrid larvæ of the cross *P. kasloensis* ♂ x *P. gloveri* ♀ in their last instar have all of the dorsal tubercles a bright coral red whereas the homo-

¹³Cockle, J. W. *Entomological News*, Vol. 19, July 1908, p. 340.

logous tubercles of *P. gloveri* are always yellow. Further, the hybrid larvæ from the cross *P. kasloensis* ♂ x *P. cecropia* ♀ in their last three instars have the dorsal tubercles on segments two, three and four bright red, and the remaining dorsal tubercles a bright pinkish-orange, about the shade known as tango. This seems to indicate that the dorsal tubercles of *P. kasloensis* are either red or reddish-orange in all of the last three instars.

Distribution: *Platysamia kasloensis* is found throughout northern Idaho, southeastern British Columbia and western Montana. It intergrades with *P. euryalis* on the west and with *P. gloveri* on the east. Later in this paper it will be shown that *P. kasloensis* itself is the intergrade between these last two species.

***Platysamia cedrosensis* (Cockerell)**

The variety *cedrosensis* was described in the same footnote as was *kasloensis*.

"*S. rubra cedrosensis* _____, marked "Cedars I," (evidently Cedros I) Mexico. Male. Margins of upper side of wings broadly and suffusedly blackened, the submarginal markings almost entirely lost; ocellus of primaries smallish; discal mark on hind wings longer and more slender than in *kasloensis*; beneath the wings are very black, but the region basad of the bands is suffused with brownish vinaceous."

Cockerell's types were not marked because they were named after he had left the Museum and there is no specimen in the U. S. National Museum, where the type is supposed to be, that bears a label "Cedars I." The only specimen, unlabeled, that comes close to fitting the description is one of the *kasloensis* type, whose wing tips appear to have been blackened with soot as is characteristic of a moth that has been flying around an oil lantern. In fact the microscope revealed that the darkening of the outer third of the wings of this particular specimen was due to soot. Whether the type has been destroyed or this is it, we cannot say. Dr. Cockerell believes that it is not. Until other specimens are obtained from the type locality or near it, the form *cedrosensis*, like *winonah*, must remain merely a "list" name.

ABERRATIONS

The usual color aberrations caused by somatic mutation or by the failure of some developmental process occur in this genus. In *P. cecropia* the red may be replaced by yellow, or the brown and black

be replaced by yellow and orange. A fairly common aberration in *P. gloveri* and *P. nokomis* is a general suffusion of white hairlike scales over the surface of one or more wings, which gives them a mouldy appearance. The discal spots may become obsolete in all of the species. There also occur 'breaks' in which a part of the pattern becomes distorted without a corresponding distortion of the wing membrane. These 'breaks' appear more often in the hybrids than in the pure species.

The effect of cold applied to the pupa at the time of scale formation results in a thinly scaled, semitransparent condition; in an increase of red pigment and its migration towards the base of the wing; and in an increase of black pigment and its migration towards the margin. This produces a reduction or elimination of the white areas and a general haziness of pattern. The mechanism of this shifting of pigment, if indeed it takes place, is unknown, but the phenomena have been observed in other forms, particularly the Nymphalidæ.

SUMMARY

If we still refrain from distinguishing between species and form, there are eight names applied to the various forms of the genus *Platysamia*; *P. cecropia*, *P. columbia*, *P. nokomis*, *P. gloveri*, *P. kasloensis* and *P. euryalis* representing groups of organisms found distributed throughout temperate North America in the manner indicated on the accompanying map. The other two names, *P. winonah* and *P. cedrosensis* are represented by single specimens, both of which have been lost. Until more specimens are taken, we may disregard these two names.

The forms may be distinguished as follows: *P. cecropia* by its grizzled ground color, by its tapering extradiscal line on the fore wing and by the more or less wide red outside border to the extradiscal line on the hind wing; *P. columbia* by its submelanic ground color, by its white extradiscal line reaching to the costa on the fore wing and by the absence or near absence of red bordering this line on the hind wing. While an experienced lepidopterist can distinguish between *P. nokomis* and *P. gloveri*, there is no character that can be cited as separating them, although the former is much less variable than the latter. Both forms have a red ground color inside the extradiscal line and a pure grey ground color outside it. Both have



FIG. 1. Reproduced from "University of Pittsburgh Bulletin" (Graduate School Abstracts, Vol. X), Vol. 31, 1934, p. 347.

approximately reniform discal spots. *P. euryalis* is distinguished by its brick red ground color, by its long comma shaped discal spots and by the absence of grey from the ground color outside of the extradiscal line. *P. kasloensis* may be distinguished from both *P. euryalis* and *P. gloveri* by the mixture of red and grey scales in the ground color outside of the extradiscal line.

The larvæ are most easily separated in the fourth instar, the distinguishing character being the color of the dorsal tubercles, although structurally, *P. columbia* has a greater hard chitinization of these tubercles than the others and *P. cecropia* has more spines. On *P. cecropia* the dorsal tubercles of segments two and three are red, the rest being straw yellow; on *P. columbia*, they are red on segments two, three and four while the remainder are yellow. On *P. nokomis* all are bright yellow; on *P. gloveri* all are yellow or all red; and on *P. euryalis*, all are yellow, or possibly salmon colored.

The cocoons are of three types. Those of *P. cecropia* are more or less smooth, tawny and pointed at both ends, the inner and outer shells being easily separated. Those of *P. gloveri*, *P. nokomis* and *P. columbia* are dark, covered with silvery ridges, pointed only at the open end and impregnated with a dark gummy substance. The cocoon of *P. euryalis* resembles that of *P. cecropia* in color and texture but is ellipsoidal, almost spherical and has a slender neck at the open end.

III. METHODS

METHODS OF COLLECTING AND CROSS BREEDING

In the early part of the work, cocoons were collected in the Fall or purchased from collectors in other localities. They were kept over winter in a cold place in order that they would not emerge before the wild moths around Pittsburgh. Males of one species were confined with females of another in cheesecloth cages of about one cubic yard capacity. This method, which was used by Miss Morton, yielded a number of crosses but many refused to mate. A second method which was more successful was the method known as 'tying out.' In it the female to be mated is tied to a protecting bush by a piece of soft string around the body between the primaries and secondaries. The only variation in the use of this time honored method was that the female was always of a species not occurring in the district. Females 'tied out' in this manner were seldom unmated.

It became evident early in the experiments that cocoons of the species other than *cecropia* could not be obtained in sufficient quantities, if at all. Also, a means for determining the nature of the insects in the zones of contact between the species was imperative. The knowledge that the females of any one species readily attract and mate with

the males of any other species in the genus, as was learned the first season, and the use of a truck for transportation of the insects solved these problems. During 1932 and 1933, collecting, breeding, and the analysis of the zones of contact, were combined into one operation.

A road was selected through the country to be explored, and virgin females (usually *P. cecropia*) were tied in the shelter of bushes sufficiently far back from the road so as to not be disturbed by traffic. These 'plants' were spaced at intervals of from five to ten miles for a distance of about a hundred miles, and camp was made in a particularly promising locality. The remaining females were placed in a wire cage on the engine hood. If there were *Platysamia* males in the neighborhood, the operator was awakened about an hour before dawn by their flapping against the top and sides of the truck as they tried to locate the females. He then caught them in his hands as they fluttered against the cage, dropped those he wished to mate into the cage and those he wished for specimens into a cyanide bottle. The rejected ones were placed in a bucket covered over with netting, to be released at dawn. The number of males dropped into the cage must always be one less than the number of females there because the attracting odor is not emitted after mating. Although the males normally remain in coitus for from fifteen to twenty hours, it has been found that two hours is sufficient for complete ensemmination. At the end of about two hours the cage was placed inside the truck and the route of the previous day retraced. The jarring of the wheels on the road soon dislodged the males and as soon as the union was broken, the male was killed and given a number. The female was placed in a small cardboard box or paper sack with the same number. Notes must be taken concerning any peculiarity of color or pattern before the female is placed in the box because she remains in there five days and batters her wings to pieces. At the end of the egg laying period the female was killed and preserved and the eggs which she had glued to the inside of the box were picked off and kept in vials until they hatched. Along the 'trapline' all the females were found mated if one was lucky. We thus got a sample male from each interval of the district covered, and a fairly complete record from the district of the camp. In this manner also, up to twenty-five cross matings have been secured in a single night. Factors which prevented mating or the securing of the males were (1) a cold night, (2) high winds which forced early separation, (3) birds, mice or ants may have

killed the female, and (4) the tied female may have been discovered by some other human.

METHODS OF REARING

The eggs hatch in from ten to twenty days, turning dark a day or two before the larvæ crawl from the shell. Experience has demonstrated that wild cherry (*Prunus serotina*) is best suited as a food plant for the hybrids regardless of upon what plant their parents feed. If this is not available, elderberry (*Sambucus*), willow (*Salix*) or alder (*Alnus*) may be used in the order named. As soon as the larvæ emerged from the shell, they were placed in a large vial with several leaves, and the vial was plugged with cloth and put in a cool place. Fresh leaves were substituted at six hour intervals, care being exercised that the tiny larvæ were not pulled from the old leaves but cut out on a small section of the leaf to which they clung. After twenty-four to thirty-six hours they were ready to be placed in the breeding cages.

The hybrids were too delicate to be reared on cut leaves in boxes and cans as the parent species may be. They had to be fed on the living food plant under ideal conditions. A cage was devised that gave the larvæ protection against all of the parasites and predators except boys and the ants. The latter were excluded by banding the trunk of the food plant with tanglefoot. The cage was constructed as follows: thirty inch, sixteen mesh window screen was cut into thirty-six inch lengths. Pieces of strong cloth twelve to fifteen inches wide were sewn to the long sides. The short sides were then tacked to a stick of wood so as to form a cylinder, the ends of which were cloth. The edges of the cloth were then sewn together to complete the cylinder which was open at both ends. In use, a branch was selected and violently shaken and carefully inspected lest a spider or reduvid bug remain and be confined with the larvæ. The cage was then slipped over the branch and the cloth tied firmly around the stem. The larvæ were then introduced through the free end and the end tied shut. This arrangement permitted the larvæ to feed on the living host under natural conditions with all of the attendant advantages but at the same time afforded complete protection against predators and insect parasites. The cage was examined from day to day and when nearly all of the leaves had been eaten, it was removed to another branch. The caterpillars, which by that time were in the second instar and had reached a length of about three-quarters of an inch, were trans-

ferred by cutting out the pieces of the leaf to which they clung or by rolling them off the twigs. Great care was exercised in order that the delicate prolegs might not be torn. If the caterpillar was moulting, the entire twig was cut off and carefully placed on the fresh foliage. As the caterpillars grew, fewer and fewer were kept in a single cage, until during the last instar, when they attained a length of from three to five inches, no more than ten were kept in each cage.

METHODS OF PATTERN AND COLOR ANALYSIS

Intergrades were found in the zones of contact, particularly in the contact between *P. euryalis* and *P. gloveri*. When the specimens were pinned to a large board according to their geographic distribution, the way in which they intergraded immediately struck the eye. Such a demonstration could not be put on paper, so a statistical method was devised for illustrating this blending. The specimens were classified according to the degree to which they resembled one or the other of the supposed parent species. For instance, the two most important differences between *P. euryalis* and *P. gloveri* are the shapes of the discal spots on the hind wing and the color of the area just outside of the extradiscal line. The discal spots of *P. gloveri* are reniform (except in its most southern range) while those of *P. euryalis* are quite elongated. The area in question is red with no gray in *P. euryalis* and the reverse in *P. gloveri*. In the analysis of the discal spots, since the size varies greatly in both species, no single measurement such as length or area was found to be of any value for comparison and a ratio of length to width, which would have eliminated the factor of variable size was found to depend on from what points the measurements were made. A satisfactory measurement, the ratio of average width to longest length, was obtained in the following manner. The spots were carefully traced using a camera lucida and the areas thus obtained were measured with a planimeter. This area divided by the square of its longest length gave the desired index of the shape of the spots. The ratios thus obtained were plotted against the geographic distribution as is shown in Chart II, page 208. The other character (color) did not yield to so objective an analysis. The gradations between the gray and red were divided into eighteen approximately equal classes and the specimens plotted by classes against geographic distribution as recorded in Chart I, page 207.

Because of the extreme variability of *P. cecropia*, and the small

amount of intergradation detectable, no such comparison could be made in the contacts between *P. cecropia* on one hand and *P. columbia* or *P. nokomis* on the other in the eastern zone of contact.

METHOD OF GENITALIC ANALYSIS

Mr. Foster H. Benjamin of the United States Bureau of Entomology and Plant Quarantine pointed out that there occur instances where two species intergrade in color and pattern but are quite distinct in their genitalia. He suggested that before any proof could be established that intergradation was due to hybridization, this possibility must be eliminated. He very generously devoted considerable time to instructing the writer in the art of preparing slides of the genitalia of Lepidoptera, the Saturniidae in particular.

The male genitalia were prepared as follows: The insect was relaxed and a scalpel inserted into the underside of the abdomen just ahead of the genitalia. The latter was then pried off leaving the rest of the body undisturbed. This 'tip' was then either soaked over night or boiled for ten to fifteen minutes in a ten per cent solution of potassium hydroxide. This treatment destroyed the soft tissues and to a certain extent bleached the chitin. The genitalia were then placed in water and all vestiges of soft tissues teased out under a binocular microscope. When the dissection was finished, all scales and scale-like hairs, all fat and other tissue had been removed leaving only the chitin. The dissection was then dehydrated by dropping into 95 per cent alcohol where it remained half an hour. The valves were then spread open as far as possible without distorting the parts and oil of cloves dropped on. The oil of cloves serves the double purpose of finishing the dehydration and hardening the tissue. After soaking in this reagent for half an hour, the tissue was placed in xylol for a similar period and then mounted in a deep balsam cell on a slide and covered with a cover slip. Because of the comparatively large size of the *Platysamia* genitalia the cell had to be made from one and a half to two millimeters deep. So deep a cell would require years to dry, so as soon as the slide became set, it was cleaned and the cell sealed with celloidin.

The female genitalia were prepared in much the same way but have not been used in this report because no clear cut differences were found between the most divergent species.

SUMMARY

Since the color patterns, morphology and distribution of the various forms of the *Platysamia* suggested hybridization, the following methods were devised or borrowed from other workers for the purpose of analyzing the genus. Cross matings were secured either by confining the different forms together in wire screen or cheesecloth cages or by tying out a female to a bush in the territory of another form. The hybrids were reared in specially designed wire and cloth cages on the living food plant. Samples of the indigenous males of the zones of intergradation or zones of contact between two forms were obtained by tying out congeneric virgin females at intervals in the territory. Intergrades were analyzed by determining to what degree the characters that differentiate the supposed parent forms were present and plotting this against the geographic distribution. Identifications of the species were checked by examination of the male genitalia.

IV. OBSERVATIONS

A. BREEDING EXPERIMENTS

TIME OF FLIGHT AND NORMAL MATINGS

The moths of the family Saturniidae are elinguate in the adult and consequently very short lived. A mated female will live about five days, and seven or eight if unmated. The male lives a little longer. The span of life is lengthened by cold and shortened by heat as would be expected since temperature controls the rate of metabolism and consequently the rate of depletion of stored food. A life of fourteen days is recorded for *Actias selene*.¹⁴

Because of the short period of flight, the eggs and sperm are fully formed while the moth is in the pupa and are ready for fertilization immediately after eclosure. Normally the female mates the first night after emergence but can be mated on any night up to four or five days of age. Mating of the species of *Platysamia* normally takes place just before or just after dawn. Rau¹⁵ reports that the time of flight for *P. cecropia* in the latitude of St. Louis, Missouri, is sharply

¹⁴Klaue, Dr. Wolfgang, "Die Winterzucht von *Actias selene* (Lep.)," *Entomologische Zeitschrift*. Stuttgart. Vol. 44, pp. 40-42.

¹⁵Rau, Phil. and Rau, Nellie L., "The Sex Attraction and Rhythmic Periodicity in Giant Saturniid Moths." *Transactions of the Academy of Science of St. Louis*, Vol. XXVI, No. 2, 1929.

confined between the hours of 3:30 and 4:30 A.M., except in a few cases in which moonlight simulates the light conditions of early dawn. *Platysamia euryalis*, *P. kasloensis* and *P. gloveri* in Idaho and western Montana also fly just before sunrise, the flight starting at or just before the first lightening of dawn and continuing until just before the sun itself appears. *Platysamia columbia* in Ontario and Manitoba and *P. nokomis* in Manitoba fly under the same conditions. *Platysamia cecropia*, on the whole, flies at dawn, but I have secured matings in the early evening and have taken males at light (rarely), also in the evening. The flight in these exceptional cases may have been influenced by moonlight; of this I have no record. On the fifth of June, 1933, in a tamarack swamp in Claire County, Michigan, a few *P. cecropia* females attracted a number of *P. cecropia* males about two hours after dark. A dense fog had settled over the swamp.

The attracting medium is a chemical emanation, as proven beyond doubt by Rau and others.¹⁶ It is unlikely that it is the characteristic odor perceptible to man since the sexual emanation is stopped as soon as coition begins, while the odor remains. The male flies against the wind and usually goes past the female on the first try. Having thus lost the scent he drops back until he is down wind from the female and tries again. There is apparently no selection on the part of the female. She takes the first male that reaches her. Coition usually lasts until the following evening when the female becomes active and dislodges the male which then flies away. This long union is due to the daylight period of inactivity, an hour or so giving ample time for complete insemination.

The mated female *flies throughout the night* laying her eggs in groups of from three to six, usually on the top surface of a leaf or on twigs.

RECORD OF EXPERIMENTAL CROSS MATINGS

Cross Matings in Confinement: In the attempts to secure crosses between various Saturniidæ and between various American and Palearctic Sphingidæ in 1930, three crosses were obtained between *Platysamia cecropia* males and *P. gloveri* females confined together in cheesecloth cages indoors. There was a slight current of air through the cage.

¹⁶Collins, C. W. and Potts, S. F. "Attractants for the Flying Gypsy Moths as an Aid in Locating New Infestations." *Technical Bulletin No. 335, U. S. Department of Agriculture*, 1932.

In the Spring of 1931 with a larger and more varied supply of cocoons a number of matings were secured using cheesecloth cages placed out of doors. Two cages were placed together so that the wind would blow from the female of one species past the female of another species to the male of the first species. Before the weather became warm enough to place the moths outside, a few were kept in cages in a room having a single north window. On the seventh of May in this cage a *P. cecropia* male mated with a *P. gloveri* female, whose wings had not yet completed expanding, at 5:30 P.M., long before the light had decreased to the intensity normally required for activity in this genus. In the outside cages the following cross matings were obtained: *P. gloveri* ♂ x *P. cecropia* ♀ (2); *P. cecropia* ♂ x *P. gloveri* ♀ (4); *P. nokomis* ♂ x *P. cecropia* ♀; *P. cecropia* ♂ x *P. nokomis* ♀; *P. euryalis* ♂ x *P. gloveri* ♀; *P. euryalis* ♂ x *Actias selene* ♀; *P. cecropia* ♂ x *Samia walkeri advena* ♀; and *Samia walkeri advena* ♂ x *Callosamia promethea* ♀.

All of the above matings proved fertile except the intergeneric crosses, but because of inexperience in rearing and to other extrinsic causes none were reared to maturity except the product of some of the *gloveri-cecropia* crosses.

In connection with the survey trip through the zone of contact between *Platysamia euryalis* and *P. gloveri* in Idaho and Montana during 1932, many cross matings were secured between various species while they were confined out of doors in a large cheesecloth cage five by eight by three feet, or in wire cages measuring eighteen inches on a side. Most of the matings involving hybrids reared the preceding year were procured in this manner. The matings included: *P. cecropia* ♂ x *P. gloveri* ♀ (7); *P. gloveri* ♂ x *P. cecropia* ♀ (8); *P. cecropia-gloveri* hybrid ♂ x *P. cecropia* ♀; *P. cecropia* ♂ x *P. cecropia-gloveri* hybrid ♀ (2); *P. gloveri* ♂ x *P. cecropia-gloveri* hybrid ♀ (4); *P. cecropia-gloveri* hybrid ♂ x *P. cecropia-gloveri* hybrid ♀ (2); and *P. cecropia* ♂ x *Telea polyphemus* ♀.

Although the hybrid females were as large and active as the normal *P. gloveri* and *P. cecropia* females and with fully as large abdomens, the eggs laid were few, the maximum being seventy-eight as compared with more than two hundred normally laid by the pure species. The cross of a hybrid male to a *P. cecropia* female produced 203 eggs, ninety per cent of which hatched.

Matings in the field: Experiments at Slippery Rock, Pennsylvania. It proved much easier to obtain matings between females of various species and males of the local species by tying out the female and permitting her to attract a wild mate than to secure the same type of cross with the principals confined in a cage. The first of these experiments took place near Slippery Rock, Pennsylvania, on June 19, 1931. Three females of *Actias selene*, two of *Tropea luna*, one of *Platysamia euryalis*, one of *P. nokomis*, and three of *P. gloveri* were anchored to shrubs at considerable intervals by tying soft string around the thorax. Wild *T. luna* males mated with the *T. luna* females during the night. *P. cecropia* males mated with two of the *P. gloveri* just before daybreak, and to the *P. nokomis* and *P. euryalis* females after the light had gotten quite bright. The *Actias selene* and one old *P. gloveri* remained unmated. All of the mated pairs remained together during a forty-five mile automobile trip back to Pittsburgh.

Experiments in Utah, Idaho and Montana: The Slippery Rock experiments demonstrated first, that cross matings could be obtained in nature as easily as normal matings and second, that a female of any segregation of the genus could be used as a "Bait" to obtain a sample of the congeneric male indigenous to any given area. Accordingly, an extended motor trip was undertaken to explore the most promising zone of contact between the various species of the genus *Platysamia*, namely the contact between *P. euryalis* and *P. gloveri* in northern Idaho and western Montana.

The writer left for Utah on the twenty-second of March, 1932, with about 300 cocoons of *P. cecropia*, those of the hybrids reared the preceding season and some cocoons of other Saturniidæ. The month of April was spent in collecting cocoons of *P. gloveri* in Utah, and in other pursuits not directly connected with the present work. One bit of information gleaned stated that the *P. gloveri* of southern Utah around Panguitch and Zion Park were different from those of the Salt Lake region. Acting upon this information, three *P. gloveri* and three *P. cecropia* female cocoons were sent to Ranger Harold Russell of Springdale, Utah, with instructions as to how to secure cross matings and take care of the eggs. Five matings were secured in spite of the lateness of the season, and the eggs along with the dead parents were shipped to Idaho where the larvæ were reared with those bred from crosses in that region. The *P. gloveri* males thus obtained from southernmost Utah together with a female caught in Zion Park by

a boy scout and given to me (unfortunately dead) differ so slightly from the Salt Lake *P. gloveri* that separation is impractical.

The main objective of the expedition was the region centering around the Bitterroot Mountains in northern Idaho and Montana. The weather was much too severe in early May for breeding, so two base camps were set up, one along Pine Creek near Enaville, Idaho, at an elevation of 2400 feet and one at an abandoned mine near Lookout Pass in the Bitterroot Mountains close to the Idaho-Montana line at an elevation of 4500 feet. The *Platysamia* began to fly during the last week of May.

The plan was to collect samples of the *Platysamia* population along a line coinciding approximately with U. S. highway No. 10 from a point at the western end where the males caught would prove to be *Platysamia euryalis* to an eastern terminus where the males caught proved to be purely *P. gloveri*. This plan was carried out as closely as conditions permitted. The western terminus proved to be Lake Coeur d'Alene in Idaho and the eastern one about twenty miles east of Helena, Montana. The route and collecting stations are shown on the map in connection with Chart II.

The first cross mating was secured on May 18, at Enaville and the last on July third at Lookout Pass. At each of the stations along the route one or more wild males were taken except along the section between Turah and Drummond, in Montana, where high winds separated the mated pairs before they could be collected in the morning. That mating took place was proven by the fertility of the eggs laid by the females. A few of the moths tied out were lost to birds and ants. On the eastern slope of the continental divide near Helena, Montana, a female of *P. cecropia* and one of *P. gloveri* were tied in a clump of willows. Next morning the *P. cecropia* had a *P. gloveri* mate while the *P. gloveri* female remained unmated. The males taken in this manner are listed with an analysis of their specific characters in Charts I and II on pages 207-208. They mated with *P. cecropia* from Pennsylvania (26 matings), *P. gloveri* from Utah (10 matings), *Callosamia angulifera* (2 matings), *P. cecropia-gloveri* hybrid (2 matings) and a *Samia walkeri advena*.

Experiments in Michigan, Minnesota, Manitoba and Ontario: In the Spring of 1933 a survey was made along the contact between *Platysamia cecropia*, *P. columbia* and *P. nokomis*. Special permits from the Canadian and United States Departments of Agriculture

authorized the transportation of the experimental insects either way across the border. A late start made a very hasty survey necessary. The route and breeding stations are indicated on the accompanying map. Cold and high winds handicapped the work but sufficient data



FIG. 2. Route of the survey of the Canadian Zone of Contact showing collecting stations.

were collected to permit tentative conclusions. Nine matings between *Platysamia columbia* males and *P. cecropia* females, one between a *P. columbia* male and a *P. gloveri* female and four between *P. nokomis* males and *P. cecropia* females were secured. About ten miles west of Winnipeg two *P. cecropia* females were tied to opposite sides of the same bush. In the morning one had mated to a male *P. cecropia* and the other to a male *P. nokomis*. Again, about twelve miles north of North Bay, Ontario, a single *P. columbia* male and nine *P. cecropia* males came to the female *P. cecropia* in the emergence cage. Except for these two instances, the males attracted at any given place were always of one species only. Near Whitemouth, Manitoba, *P. columbia* males came in great numbers from a tamarack swamp and in their frenzied efforts to reach the caged *P. cecropia* females, two mistook each other for females and were found in the morning with their claspers interlocked.

In Michigan and Minnesota, even though tests were made in extensive tamarack bogs, no *P. columbia* were taken. In northern Ontario only two *P. columbia* were collected in two of the few places where moderate sized tamarack (*Larix americana*) remains. According to the men in the forestry service, the tamarack had been all killed by the larch sawfly about thirty years before. This may partially account for the extreme scarcity of *P. columbia*. The males collected were 59 *P. columbia*, 21 *P. nokomis* and 57 *P. cecropia*.

Further Matings of Hybrids and Secondary Hybrids: In the Spring of 1934, males of the hybrids *P. columbia-cecropia* and *P. nokomis-cecropia* were crossed with *P. cecropia* females and the offspring reared to maturity. The eggs of the reciprocal crosses were sterile.

In the season of 1935, the secondary hybrids thus produced were reciprocally crossed with *P. cecropia* and *P. columbia*. They were also inbred. All proved sterile except two matings involving secondary hybrids *as both parents*. From sixty-three eggs a total of thirteen caterpillars hatched. Of these, ten reached the third instar and one reached the fourth instar, but all died, presumably of the disease that killed ninety per cent of the 1935 caterpillars of pure species as well as hybrids. The other cross matings numbered thirty-three and involved *P. cecropia*, *P. columbia*, *P. gloveri* and *P. kasloensis*.

SUMMARY OF BREEDING EXPERIMENTS

The moths of the genus *Platysamia* mate during the two hours preceding dawn, the male being attracted to the female by a chemical emanation analogous to scent. A female *Platysamia* will attract any congeneric male and also a few of the males of related genera. Taking advantage of these facts, sixty-one cross matings were made in the various zones of contact between the species. In the process of securing these cross matings samples of the moths found in each locality were also obtained. Seventy-four cross matings, some of which involved primary or secondary hybrids were made in confinement to supplement the crosses made in natural surroundings.

B. VIABILITY OF THE HYBRIDS

PER CENT OF HATCH

In the crosses between the various natural forms of the genus *Platysamia* only a few (four) were infertile. That is, in only four cross

matings did the eggs collapse two or three days after oviposition as normally occurs with the eggs of unmated females. Early collapse of the eggs also indicated that the *Samia walkeri advena* x *Platysamia cecropia* cross, the *Callosamia promethea* x *S. walkeri advena* cross, the *Actias selene* x *Platysamia euryalis* cross and the *Telea polyphemus* x *P. cecropia* crosses were also infertile.

The eggs of the remaining crosses underwent at least some differentiation. In about 30 per cent of the crosses between natural forms of *Platysamia*, in all of the crosses involving primary hybrid females, in about half of those involving secondary hybrids and in the *Callosamia angulifera* x *Platysamia kasloensis* cross, the eggs developed almost to the hatching point. They did not immediately collapse, the normal depression in the top of the egg appeared, and in from ten to fifteen days they turned dark, but no larvæ emerged from the shells. (Normally the larva eats its way out of the shell on the day following that on which the egg becomes dark.) After about fifteen days the eggs slowly collapsed.

With few exceptions, the remaining broods produced larvæ from about 95 per cent of the eggs. This is the normal expectancy for pure species matings. One particular exception was the cross between a *Platysamia gloveri* ♂ from Zion Park, Utah, and a *P. cecropia* ♀ from New York. From the eggs of this cross only 18 larvæ emerged.

FACTORS IN LARVAL MORTALITY

When this work was first undertaken, the writer had had no experience in rearing Lepidopterous larvæ in confinement, and as a result most of the early hybrids were lost through (1) overcrowding, (2) too moist or too wilted food, (3) lack of ventilation, and (4) disease. When reared out of doors in the conventional cheesecloth sleeves, the larvæ fell prey to ants, spiders, reduvid bugs and birds. The use of the wire cage described previously practically eliminated all of these hazards except disease.

Many of the hybrid larvæ refused to eat, some not touching the leaf, others merely biting holes in it. The loss from this source amounted to an average of about ten per cent of all the larvæ that hatched. Sometimes the larva would feed almost to the first ecdysis and then stop.

Even under ideal conditions, the hybrid larvæ were less resistant than the larvæ of pure species reared in adjacent cages. They were

subject to three presumably epidemic diseases, the names and causes of which are unknown to me. In the first or second instars, the larva would be found flattened down to the leaf or stem with a film of liquid extending out from in under it, or the caterpillar would lose hold with its prolegs and stop feeding. In such broods few of the larvæ reached the fourth instar and none pupated, even when the apparently healthy larvæ were segregated when the first symptoms appeared in the brood. A second disease that claimed heavy toll usually appeared in the fourth or fifth instars. The apparently healthy larva regurgitated a greenish liquid which soon turned brown, stopped eating and then either dried up or became liquified. One larva, kept in a humid container, lived several weeks but did not resume feeding. In 1935, a brood of *P. kasloensis* ♂ x *P. gloveri* ♀ was separated into four parts before hatching and each part reared on trees separated by at least a quarter of a mile. A few were also permitted to feed unprotected exactly in the manner that the wild larvæ feed. All of these larvæ developed the symptoms described above at the same time. The disease also destroyed broods of typical *P. cecropia* and the way in which it appeared almost simultaneously in all members of a brood seemed to indicate that the causal agent was transmitted with the egg, probably in the cementing material on the outside. The third disease was characterized by the appearance of dark blotches along the sides of the larva and developed only in full grown specimens. All of these "diseases," as is to be expected with caterpillar sicknesses, ended fatally.

In addition to the greater susceptibility to disease, the hybrid larvæ had thinner, more delicate cuticula than the pure species, resulting in a greater proportion of deaths by tearing during ecdysis. Other irregularities included a failure to even attempt to molt. In this case the first stage caterpillar continued to feed after the others had molted until it had more than doubled the size normally attained by that instar, and finally had to stop because its skin would not stretch any farther.

In 1932, the hybrids were reared at Lookout Pass in the Bitterroot Mountains and had only reached the last instar when the time arrived for the return to Pittsburgh. Several thousand larvæ, three to four inches long were transported more than two thousand miles by truck, a ten day trip. Four different species of willow were used to feed the caterpillars along the way. The mortality, as would be

expected, was enormous and the hybrids that did survive were of small size. Imagoes of almost all of the broods were secured, however, except the one that was most important to the study, namely the F_2 back cross between a *P. gloveri-cecropia* hybrid male and a *P. cecropia* female. The larvæ of this cross fed normally, had a low rate of mortality and went into the last instar in apparently perfect condition, but did not survive the ten day truck ride.

In 1934, other back crosses were successfully reared. They were (*P. columbia* ♂ x *P. cecropia* ♀) ♂ x *P. cecropia* ♀ and (*P. nokomis* ♂ x *P. cecropia* ♀) ♂ x *P. cecropia* ♀. The imagoes from these crosses were partially fertile in both sexes, but the offspring did not reach the fourth instar.

SUMMARY

In a very few of the hybrid crosses fertilization was not secured and in about thirty per cent, development stopped just before the time of hatching. With few exceptions, the broods that hatched produced the same percentage of viable larvæ as did the pure species broods, but they had a slightly greater susceptibility to disease. Most of the hybrid larvæ, as well as a similar proportion of the pure species, were lost through causes independent of the genetic composition of the animals, such causes as improper feeding and epidemic disease.

C. MORPHOLOGY AND BIOLOGY OF THE HYBRIDS

LARVAL INHERITANCE

When first hatched and throughout the first instar the hybrids are indistinguishable from the first stage larvæ of the species of the female parent. In the second, third, and fourth instars, the hybrid may resemble one or the other of the parents, usually alternating from one to the other. The resemblance is seldom complete. In the last instar the color has the appearance of being caused by the superposition of the larval patterns of both parent species. One cannot rely strongly on larval colors as a criterion for distinguishing the species of the genus *Platysamia* and even less for the hybrids, in spite of the excellent descriptions and beautiful illustrations in Dr. Packard's monograph. There is a great deal of variability. Two full grown larvæ were collected on the University of Pittsburgh campus that had the characters of *P. gloveri-cecropia* hybrids, in fact, had they been taken near my rearing grounds, I would have thought that they had

escaped from a hybrid cage, but the one that emerged was a typical *P. cecropia*. There is also the example from Glacier Park cited in the general description of the form *P. gloveri*, which had neither the appearance of *P. gloveri*, or that of a *P. gloveri*-*P. kasloensis* hybrid, but emerged a typical Montana *P. gloveri*.

ADULT COLOR AND PATTERN

The adult hybrids are intermediate between the parents in color and pattern. The individuals of a particular brood are remarkably uniform, so uniform that the specimens may be sorted as to brood without recourse to the labels. The variation between the broods, however, is quite marked; it is much greater than the variation within either parent species. This variability makes the assignment of a name to the offspring of a particular cross¹⁷ impractical, even if it were desirable to do so. There does not appear to be any character that shows dominance. There is a slight disposition towards a greater inheritance from the male than from the female, particularly in the shape of the discal spots. In reciprocal crosses between *P. cecropia* as one parent and *P. gloveri* as the other, the shape of these spots has been very close to that of the spots of the male. The same has been true of other crosses.

SIZE AND VIGOR

Imagoes of hybrids reared in Pittsburgh were equal to normal specimens of the parent species in size and vigor. Hybrids between *P. cecropia* and either *P. columbia* or *P. nokomis* were intermediate in size between the parents. The mating reactions, periods of activity, and length of life were normal for the genus. Only those that were improperly fed were small and weak.

SEX RATIO AND FERTILITY

The sex ratio of the pupæ was approximately one to one. Most of the male pupæ of hybrids reared in 1931 were sent to Italy to Dr. H. Bytinsky-Salz for cytological study so that females predominated among those that emerged in Idaho. Among the other hybrids that have emerged to date, there has been a slight, but not significant excess of females.

¹⁷The hybrid *P. cecropia* ♂ x *P. gloveri* ♀ has been named *P. griffithsi* by Tutt.

Among the *P. cecropia* ♂ x *P. gloveri* ♀ hybrids to emerge in 1932 was a gynandromorph. (plate XVIII, fig. 1). The antennæ were those of a male. There was a distortion in the pattern of the right fore wing, the extradiscal band having spread proximally in its middle portion. The external genitalia were poorly developed and covered with a cheesy substance. They were more female than male. There was a suggestion of an ovipositor and a chitinized tube leading into the abdomen from beneath it that resembled the tube of the bursa copulatrix, but there was no bursa inside and no guide plate outside. On either side of these central structures were slight out pocketings that were in the position of the male harpe. Internally, the genitalia were as poorly developed as externally. There was a small ovoid structure resembling the testis of a third instar caterpillar attached to the dorsal wall on the left side but with no ducts connected to it. On the right side was a system of ducts resembling those of a male but ending in an organ that resembled a small ovary in that it appeared to be a bundle of tubes tapering to a point.

The hybrid females so far produced that have not been stunted by improper feeding have had abdomens fully as large as females of the parent species, but they have laid few or no eggs. The largest number laid has been seventy-eight as against a normal two hundred to two hundred and fifty for the pure species. This failure to lay eggs has not been due to a retention of the eggs, because the hybrid moth usually laid one or two "runts" after she had laid the normal sized ones, indicating that all had been laid. Females of the hybrid *P. cecropia* ♂ x *P. gloveri* ♀ were mated to *P. gloveri*, *P. cecropia*, *P. kasloensis* and brother hybrid males but, although the eggs always began to develop, none hatched. On the other hand, the male hybrid, when crossed back to one of the parent species (*P. cecropia*), produced offspring that reached the last instar and were then lost through circumstances that destroyed even the pure species larvæ.

The females of the hybrids *P. columbia* ♂ x *P. cecropia* ♀ and *P. nokomis* ♂ x *P. cecropia* ♀ as well as the single female from the cross *P. columbia* ♂ x *P. gloveri* ♀ were also sterile, in fact, only a few contained any eggs whatever. The males, though, were fertile and several broods were reared from back crosses to *P. cecropia* females. The imagoes ($\frac{3}{4}$ *cecropia*, $\frac{1}{4}$ *columbia* or *nokomis*) from these crosses were normal in size and mating reactions. Most of them were partly sterile, the eggs developing part way but not hatching, but

thirteen of the twenty-eight eggs produced from this cross
 $P. \frac{(columbia \text{ ♂ } \times cecropia \text{ ♀ }) \text{ ♂ }}{cecropia \text{ ♀ }} \times P. \frac{(columbia \text{ ♂ } \times cecropia \text{ ♀ }) \text{ ♂ }}{cecropia \text{ ♀ }}$ ♀
hatched and one reached the third instar.

SUMMARY

The hybrids, when properly reared, were as large and active as the parent species and had normal reactions. The females of the primary hybrids were all sterile, or at least none of their eggs hatched, but the males were fertile. Both sexes of the secondary (back cross) hybrids were quite variable as to fertility but a male and a female proved fertile. This was in hybrids between species that meet but do not intergrade in nature.

D. ZONES OF CONTACT AND INTERGRADATION

THE NORTHWESTERN CONTACT

Where ever the various forms of the genus *Platysamia* come into contact there occurs hybridization and intergradation to a greater or

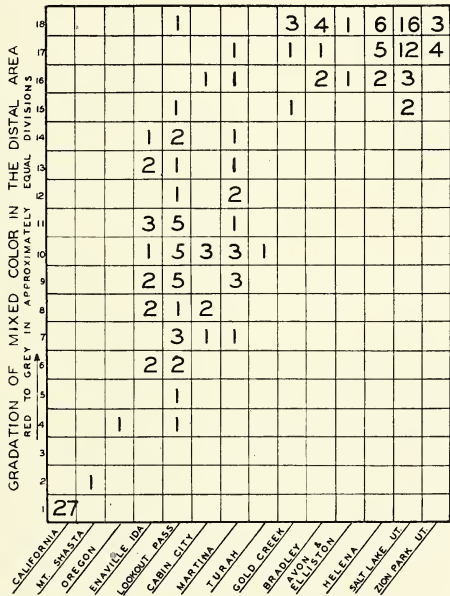


CHART I. Intergradation between *Platysamia coryalis* and *P. gloveri* as indicated by the color at the distal area.

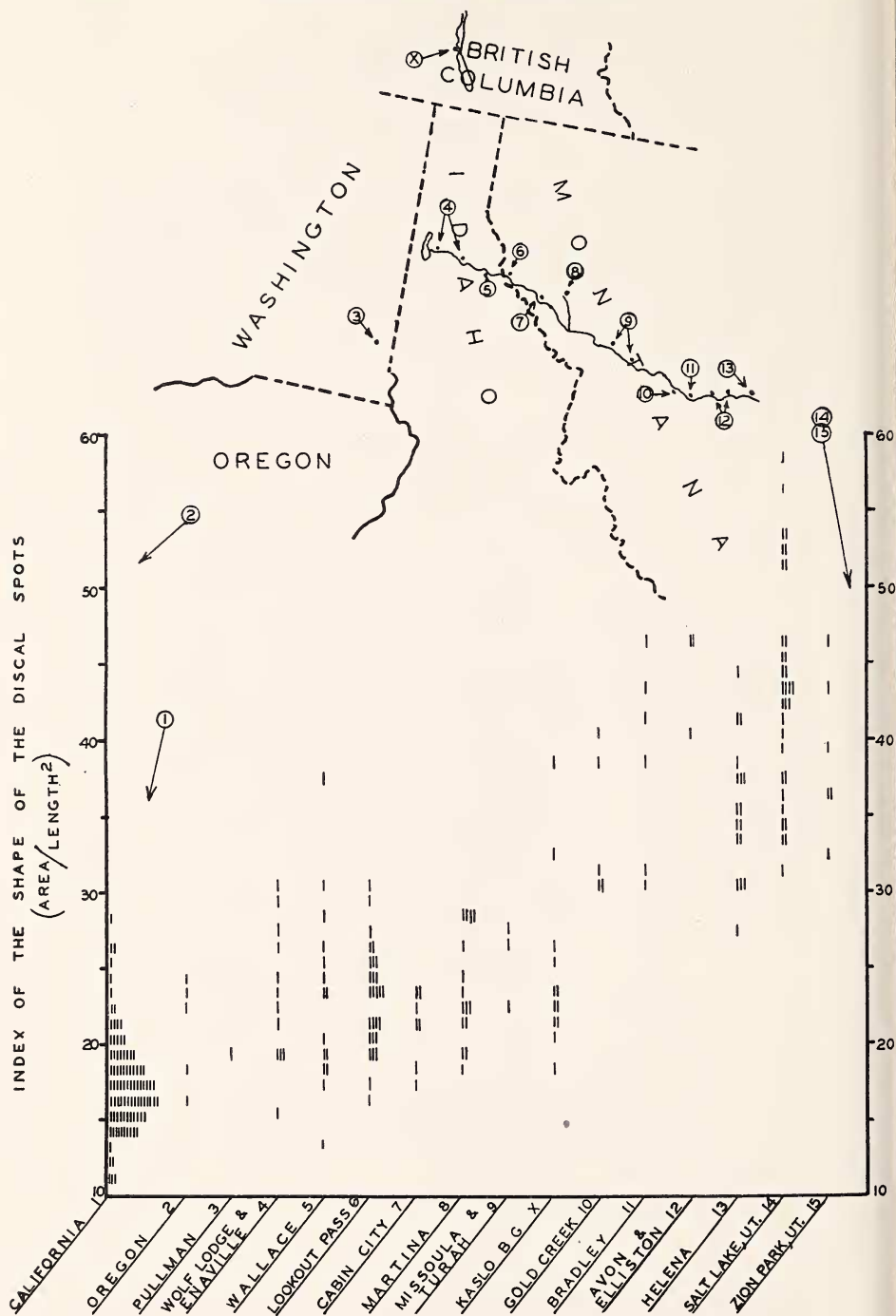


CHART II. Intergradation between *Platysamia euryalis* and *P. gloveri* as indicated by the shape of the discal spots.

less degree. There is continuous intergradation from the bright California *P. euryalis* through the darker Oregon form, through the quite dark *P. kasloensis* in Idaho, southeastern British Columbia and western Montana to typical *P. gloveri* in Montana. This intergradation is shown in Charts I and II. Chart I is based on one distinguishing character between *P. euryalis* and *P. gloveri*, namely the color of the distal area, all the specimens being either in the collection of the writer or in the Carnegie Museum. Chart II is based on the other character, the shape of the discal spot of the hind wing. In addition to the specimens used in Chart I, there are included measurements made from photographs of material in the collections of the United States National Museum, the Redpath Museum of Montreal, the University of Montana and of Mr. Otto Huellemann of Wallace, Idaho. The charts are arranged so as to indicate geographical position from west to east, but the chart distances have no relation to actual mileage.¹⁸ Specimens representing approximately the mid-intergrade were taken at Kaslo, British Columbia and were named *Samia rubra kasloensis* by Dr. T. D. A. Cockerell.

The charts are a feeble attempt to put on paper the intergradation that is apparent to the eye when the specimens are pinned out in approximately their geographic position. If one were to remove the labels and rearrange into a *P. euryalis* group and a *P. gloveri* group, it would be found that four of the *P. kasloensis* specimens would move over into the *P. gloveri* group, a number would be placed with the *P. euryalis* group, and the remainder would not fit into either. The *P. kasloensis* differ from all the other naturally occurring groups in that the extradiscal band often appears to be composed of two bands superimposed with the matching not quite exact.

THE SOUTHWESTERN CONTACT

Although no definite survey has been made, the meager information available seems to indicate that there is a similar intergradation in southern Arizona and southern California, between the same two species. The locale of the contact consists of isolated, parallel

¹⁸There is a gap between Turah, Montana and Drummond, Montana. A storm developed early in the morning following the night the survey was made in this district. As a result, although the females that were tied out had been mated as was indicated by their fertile eggs, no native males were obtained because they had been shaken loose by the wind before I could reach them. The two towns are in the same river valley, however, and there is no barrier whatever between them.

mountain ranges across the desert. The evidence is as follows: eight specimens of *P. gloveri* from Pima and Cochise Counties in Arizona, close to the Mexican border, that have discal lunules almost as long as those of *P. euryalis* and have pink scales in the distal area; a similar specimen (Plate XVI, fig. 1), but with shorter discal lunules, taken at Temecula, California, *west of the Coast Range*, within twenty-five miles of the Pacific, by Mr. Hans Christian; a specimen from Palm Springs in Imperial Valley on the west slope of the Sierra Madres that cannot be distinguished from *P. kasloensis* and another from Azusa, in Los Angeles County also having the characters of *P. kasloensis*. Dr. John A. Comstock has written reporting a specimen from San Fernando, California, that has gray in the distal band, and assures me that it is entirely possible that *P. euryalis* of California and *P. gloveri* of Arizona may come into contact across the Sonora Desert zone of the United States or in northern Mexico.

THE CANADIAN CONTACTS

The next most important zones of contact are those between *Platysamia nokomis* and *P. cecropia*, and between *P. columbia* and *P. cecropia* in southern Canada. There is no continuous intergradation, but if we consider *P. columbia* and *P. nokomis* as coming from the same stock as *P. gloveri*, then the shape of the discal lunules (slightly elongated and pointed) and the presence of red scales in greatly varying quantities along the distal edge of the white extradiscal band in the same position as the red band of *P. cecropia* are both characters that could have been introduced into the stock by hybridization with *P. cecropia*. Because of the great variation of *P. cecropia*, no possible influence of *P. nokomis* or *P. columbia* on it can be determined. Also because of this great variability, no clear cut differences exist between the species upon which to base an analysis of the type shown in Charts I and II. The following observed facts are of importance in a consideration of these zones of contact: (1) cross mating occurs as freely as normal matings; (2) the hybrids can be reared to the imago stage, the male hybrids are fertile and the second generation backcross hybrids may be fertile in both sexes; (3) except for very narrow zones and a few very limited eastern colonies, the three species are mutually exclusive; (4) neither *P. nokomis* or *P. columbia* occupies the entire range of its food plant, the southern parts being exclusively occupied by *P. cecropia*; (5) *P. columbia* has not been

taken for about thirty years in eastern Ontario, Quebec or New York; (6) the writer has a specimen sent from the Riding Mountains of Manitoba as *P. nokomis* that is identical with a backcross hybrid of a *P. nokomis-cecropia* male with a *P. cecropia* female. In addition to these personal observations, the following presumably accurate observations of others have been gleaned from the literature: (6) a *P. cecropia* cocoon intermediate between the cocoons of *P. cecropia* and *P. columbia* was reported from the type locality of *P. columbia*;¹⁹ (7) "One small and very dark colored male also presented by Mr. Smith from the same locality (as type of *P. columbia*) I considered first to be an intermediate form, but on comparing carefully the details I find it to be a cecropia, although a somewhat remarkable variety";²⁰ (8) a cocoon collected from larch with *P. columbia* cocoons and very similar to them that eventually produced a *P. cecropia*—hybridization suggested by the worker reporting it;²¹ (9) a *P. cecropia* type cocoon taken on maple in Montreal that produced a *P. columbia*.

Platysamia columbia and *P. nokomis* do not at the present time come into contact, a narrow spear head of *P. cecropia* having pushed down the Red River of the North between them, but some of the specimens of the former species taken at Whitemouth, Manitoba, might be considered to be intermediate between the usual *P. columbia* and *P. nokomis*, but such specimens are nearer to the Montana form of *P. gloveri* than to *P. nokomis*. In fact there are three specimens in my collection, one a *P. columbia* from Whitemouth, Manitoba, another a *P. nokomis* from Two Creeks, Manitoba, and the third a *P. gloveri* from Helena, Montana, that are identical in color and distribution of colors, differing in pattern to a less extent than do specimens taken in one locality. To be sure, not one of these specimens is quite typical of its district, but each is included within the normal range of variation of its species. *P. nokomis* is much brighter than either the Montana *P. gloveri* or the *P. columbia* to the east of it and so cannot be considered to be an intergrade between those two species.

Platysamia nokomis meets *P. gloveri* somewhere in Alberta and the

¹⁹Hagen, H. A. "On *Attacus* (Samia) *columbia* and Its Parasites," *Bull. Buffalo Soc. Nat. Sci.*, Jan. 1875.

²⁰Cook, J. A., in the Proceedings of the Annual Meeting of the Entomological Society of Ontario. *Canadian Entomologist*, Vol. 14, p. 177.

²¹Pearson, C. W. Correspondence. *Canadian Entomologist*, Vol. 6, p. 119, 1874.

intergradation is complete. Since the larval stages of the two forms are practically identical, and the food plants overlap, while both the larvæ and the food plants of *P. nokomis* differ from *P. columbia*, I believe that *P. nokomis* should be placed as a sub-species of *P. gloveri* rather than as a sub-species of *P. columbia*.

Dr. Cockerell²² has recently reported an invasion of *P. gloveri* territory at Boulder, Colorado, by *P. cecropia* and I have specimens of both of these species taken during consecutive years in the same part of the Black Hills of South Dakota. What the effect of these invasions will be remains to be discovered. The two species freely interbreed.

MATCHING OF INTERGRADES WITH HYBRIDS

Many of the specimens taken in these zones of contact have been matched by known hybrids reared in confinement. The only hybrid between *P. euryalis* and *P. gloveri* that has been reared by the writer to the imago stage is matched exactly as to pattern and color by a specimen taken at Pine Creek, Shoshone County, Idaho, and by another taken at Lookout Pass, Mineral County, Montana, both specimens typical *P. kasloensis*. In each locality other specimens were taken that are intermediate between the hybrid and *P. euryalis* and between the hybrid and *P. gloveri*. In other words, the hybrid is well within the range of variation of the specimens of *P. kasloensis* taken at the two localities.

Ten of the *P. gloveri-cecropia* hybrids can be superficially matched by *Platysamia columbia* taken at Whitemouth, Manitoba; six others match except for size; and two can be matched by a *P. nokomis* specimen. True, neither the *P. columbia* or *P. nokomis* involved are typical but they are wild stock. This comparison is not made to show that *P. columbia* or *P. nokomis* are the result of crossing *P. cecropia* and *P. gloveri* for the evidence as a whole does not warrant it, but as a suggestion as to the possible origin of certain *P. cecropia* characters present in both *P. columbia* and *P. nokomis*.

Primary hybrids between *P. cecropia* and either *P. columbia* or *P. nokomis* have too wide a red extradiscal band to be considered *P. columbia* and lack the tapering of this band on the fore wing which excludes them from being considered aberrant *P. cecropia*, but, the

²²Cockerell, T. D. A. "The Westward Spread of *Samia cecropia*." *Journal of Economic Entomology*, August 1929 and "The Spread of *Samia cecropia*," same journal, December 1929.

backcross hybrids ($\frac{3}{4}$ *P. cecropia*, $\frac{1}{4}$ *P. columbia* or *P. nokomis*) are distinguished from the typical *P. cecropia* only by the lack of taper in the extradiscal band and are matched exactly by a specimen from the Riding Mountains of Manitoba. With the exception of this last specimen, none of the caught intergrades can be considered to be of as simple a genetic constitution as the hybrid with which they were matched.

SUMMARY

There are six possible points or zones of contact between the various forms of the genus *Platysamia*: (1) in northern Idaho, southeastern British Columbia and western Montana, between *P. euryalis* and *P. gloveri*; (2) in southern Arizona and southern California, between the same two species; (3) in southern Manitoba and Saskatchewan, between *P. nokomis* and *P. cecropia*; (4) in eastern Manitoba, Ontario and in localized areas of Michigan and Maine, between *P. columbia* and *P. cecropia*; (5) in Alberta between *P. gloveri* and *P. nokomis*; and at Boulder, Colorado, and the Black Hills of South Dakota, a recently established contact between *P. gloveri* and *P. cecropia*. There is complete intergradation in zones one and five, indicated intergradation in zone two, hybridization but only partial intergradation in zones three and four, while the contacts between *P. gloveri* and *P. cecropia*, listed as zone six, are too recent to have had much effect.

E. GENITALIC ANALYSIS

I. MALE GENITALIA

General Description: The male genitalia are much alike for the entire genus. The sacculus (S), clasper (C), and harpes (H) are composed of one curved chitinous piece without sutures. When closed, the harpes cover the uncus (U) which is in the shape of a wide fork. The claspers are long and narrow and meet across the center of the genitalia leaving an approximately round opening between their ventral edges and the sacculi through which opening the ædæagus (A) protrudes. When the harpes are closed, the external surfaces of the sacculi are in contact. The anellus (An) is membranous on its dorsal side, the transtilla (T) fairly broad in the middle and arranged in the form of a flattened W, the arch serving as a dorsal guide for the ædæagus. The uncus also serves as a dorsal and lateral guide for the ædæagus. The vinculum (V) is produced into a rounded

pocket which opens posteriorly. The ædæagus is heavily chitinized and the membranous penis three lobed, one or two of which lobes bear short heavily chitinized spines.

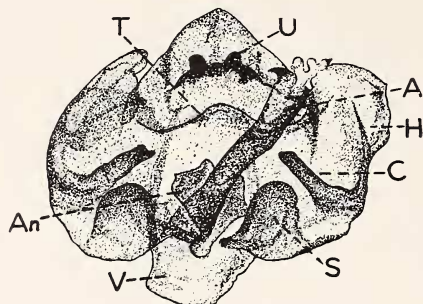


FIG. 3. Male genitalia of *Platysamia cecropia*.

A ædæagus; An anellus; C clasper; H harpe; S sacculus; T transtilla; U uncus; V vinculum.

When the harpes are opened, the sacculus folds against the inner side of the harpes, and its medial border is seen to be jointed to the lower edges of the shield shaped anellus. There is a ridge running from the base of the clasper diagonally across the dorsal lobe of the harpe on the inside which meets a similar ridge running from near the base of the transtilla. This second ridge is fringed with long hairs that extend across the opening between the ridges. A thinly chitinized membrane lines this opening and the inside of the central part of the harpe and the sacculus.

Specific Differences: As would be expected in a genus whose species freely interbreed and in certain sections intergrade, there are very slight constant differences between the genitalia of the various species. The most constant difference occurs in the spining of the ædæagus. On this basis we may separate the species into two groups, those with one spine which include *P. cecropia*, *P. euryalis*, *P. kasloensis*, and the hybrids, and those with two spines including *P. gloveri*, *P. nokomis*, and *P. columbia*.

In the single spined group *P. cecropia* has a long, narrow clasper while *P. euryalis* and *P. kasloensis* have shorter broader claspers. While the shape of the sacculus varies greatly, on the whole that of *P. cecropia* is rounded on the tip in a circular curve while that of *P. euryalis* and *P. kasloensis* is rounded in a parabolic curve.

In the double spined group, *P. gloveri* from Utah has two well developed spines, one larger than the other while *P. gloveri* of Montana, especially those specimens from Bradley and Elliston in the zone of intergradation have the second spine much reduced and in one case barely discernible. A specimen from Elliston, Montana, has only one spine but the membrane is torn, and although it appears to be all present, there is a possibility that the spine has been lost. Of seven *P. nokomis* examined four had two spines, the second one small, and three had one well developed spine and a minute trace of the second. Of eight *columbia* examined three had two well developed spines, three had one large spine and a trace of a second, while two had one spine only. The clasper is essentially the same in all the groups, and the sacculus is quite variable but tends to be intermediate in shape between the two single spined groups.

CHART III	1 Spine	1 Spine and Trace	2 Spines one small	2 Spines	Long thin Clasper	Short stout Clasper	Circular Curve Sacculus	Hyperbolic Curve Sacculus
Euryalis.....	x					x		x
Kasløensis.....	x					x		x
Gloveri intergrades.....	x	x				x	x	x
Gloveri-Montana.....			x	x		x	x?	x
Gloveri-Utah.....				x		x	x	x
Gloveri-S. Dakota.....				x		x		x
Nokomis.....		x	x			x	x	x
Columbia.....	x	x	x	x		x	x	x
Cecropia.....	x				x		x	
Kasløensis x cecropia.....	x				x			x
Kasløensis x gloveri.....	x							x
Gloveri x cecropia.....	x				x		x	

CHART III. Comparison of the male genitalia of the Platysamia.

None of the characters are very strong, that of the spines of the ædœagus being the only one upon which reliance may be placed. Upon the basis of this and the shape of the clasper, we may divide the forms into three groups: (1) *P. cecropia*, (2) *P. gloveri*, *P. nokomis* and *P. columbia*, and (3) *P. euryalis* and *P. kasloensis*. This grouping is by no means clear cut and is essentially that made on the basis of color and pattern. It will be noted that in zones where cross mating may

occur and where color and pattern intergrade, the genitalia also intergrade. On the basis of wild specimens alone it would appear that *kasloensis* is truly a subspecies of *euryalis*, but when we consider the *gloveri* ♀ x *kasloensis* ♂ hybrid and find that it also has but one spine we again open up the possibility of hybrid intergradation.

V. DISCUSSION

In the preceding parts of this report we have attempted to show the characteristics and distribution of the various forms included in the genus *Platysamia*; we have shown that intergrades exist at the points where two forms come together, that they freely interbreed when opportunity is given, and that the hybrid offspring are partly fertile.

We assume on the basis of the well established theory of descent that all of these forms have been derived from a common stock, and since they do not diverge greatly from one another, that the differentiation has been fairly recent. If we consider the data as presented we have three alternate hypotheses as to the origin of the intergrades. Let us consider particularly the intergrades present in Idaho and Montana, intermediate forms between *Platysamia gloveri* and *P. euryalis*. We may consider first that *P. euryalis* evolved from *P. gloveri* or vice-versa and that the intergrade *P. kasloensis* remains as a transition step from one species to the other. Second, we may consider that the two species arose in some other way and that the intergrades in the zone of contact are due to convergent evolution. Third, we may assume that the already differentiated species have come into contact in that particular section and that the intergrades are due to hybridization. If we do not consider the past history of the genus, any one of these explanations can be successfully defended. We must delve into the past for a solution to our problem.

We need go no farther back in geologic time than the last Glacial Age to find the key to the distribution of the genus *Platysamia*. At the beginning of the Ice Age and even earlier, the Great Plains region was covered with grass and consequentially then, as until recently, offered a barrier to the migration of moths dependent for food on trees and shrubs. We may conclude, then, that at the beginning of the advance of the ice, the progenitors of our present *Platysamia* were more or less isolated into an eastern group, east of the Great Plains and a western

group in the Rockies and Sierras. When the ice sheet reached its most southern limit, this isolation became more complete.

At its greatest extension the ice sheet reached to the sea in New



FIG. 4. Distribution of *Platysamia* during the greatest extension of glaciation.

England, across part of New Jersey, around the northern end of the Pennsylvania mountains, and ended approximately in a line parallel to and slightly north of the Ohio River, and parallel to and slightly

south of the Missouri River to the Rocky Mountains. The British Columbian ice sheet extended down into Montana and covered a part of the state of Washington. In addition there were local glaciers throughout the Rocky Mountains to southern Colorado and along the Sierras along the coast. There was also an immense névé field (perpetual snow) that extended down the Rocky Mountain system to southern Colorado and along the Sierras almost to the thirty-sixth parallel and not quite so far south along the coast ranges. This cover of perpetual ice and snow is well illustrated in the map. Immediately south of this frozen area was a belt of tundra in which the climate was about midway between that of Greenland and Alaska today.²³ Such a climate would be too rigorous for Saturniid moths. During the Pleistocene also the Gulf of Mexico extended to Nashville, Tennessee, in a narrow arm a hundred miles or more wide, the Mississippi Embayment. This formed an excellent addition to the Great Plains barrier. The belt of tundra that extended along the ice front probably reached down to this widened river and completed the isolation of the eastern and western regions.

We may surmise then that the home of the progenitors of the *Platysamia* during the last extension of the glaciers was limited to the southeastern states and to the extreme southern section of the Rocky Mountains, northern Mexico, and southern California. Although the Great Basin was arid before the Ice Age and alternately more or less arid than at present during the Ice Age,²⁴ it may have been possible that the *Platysamia* could have lived there during the more humid times. If this has been the case, there was a good connection between the western forms of the genus at least intermittently during the great glaciation.

If these reconstructions of the geography and climate of North America during the Ice Age are correct, we would have the following distribution of the *Platysamia*. The progenitors of *Platysamia cecropia* were completely isolated in the southeastern section of what is now the United States. The forerunners of *P. gloveri*, *P. columbia*, and *P. nokomis* occupied the southern Rocky Mountain system and probably all of northern Mexico, possibly extending across the Sonoran desert region during periods of decreased aridity even to the coast. The ancestors of *P. euryalis* either ranged through the southern half

²³Harshberger, John W. *Phytographic Survey of North America*, 1911.

²⁴Wright, G. F. *The Ice Age in North America*, p. 498, New York, 1902.

of California as a distinct form or formed a continuous gradation into the forerunner of *P. gloveri*.

As the ice retreated, the deciduous forests followed and with them went the *Platysamia*. The arid regions of the Great Basin formed a more or less complete barrier between *P. gloveri* and *P. euryalis*, at least in the latitude of Nevada. In the region of northern Idaho and British Columbia, the Sierras and Rocky Mountain systems come together and the desert disappears. When the two forms following these paths of migration reached this region, there was no longer any barrier between them and each spread into the territory of the other. A hybrid intergradation resulted. The matching of a hybrid by caught specimens, the ease of cross mating, and the survival of the progeny of this cross mating indicate that the intergradation is hybrid rather than due to convergence. This hybrid intergradation is known as *Platysamia kasloensis* (Ckll).

The fact that many of the specimens taken in this zone of intergradation have the extradiscal band appearing to have been made of two superimposed lines not quite coinciding, a characteristic of hybrids, is further evidence of their hybrid origin. This phenomenon is most evident when there is a distortion of the pattern as in the specimen figure 12, plate XVIII. In this hybrid, the extradiscal bands of the fore wings are distorted, but faint bands are visible through the ground color in the normal position. Such duplications are not so obvious in the *P. kasloensis* and are not to be found at all in the other forms.

In southern California and Arizona there is no continuous forested region, merely a series of parallel, isolated, sparsely covered mountain ranges with desert between them. Consequently the opportunity for free migration and interbreeding is much restricted and continuous intergradation, hybrid or otherwise, less easily established.

When the forms migrating up the Rocky Mountain system reached Canada there appeared a bridge to the eastern forests in the form of the wolf willow (*Elæagnus*) and a portion of the group became adapted to this food plant and spread over Saskatchewan and Manitoba. This portion, more or less isolated from the main species through food plant specialization, developed into the form *P. nokomis*.

There is considerable uncertainty as to the mode of origin of *Platysamia columbia*. On the basis of color, pattern, and male genitalia it is an offshoot of the Rocky Mountain (*gloveri*) stock. It is un-

doubtedly a melanic race. Either the form *P. nokomis* adopted a new host plant (*Larix*) when it reached the end of the alkaline plains or the form *P. columbia* arose separately from the parent stock at a more northern point where the Larch reaches to the Rocky Mountains.

If we accept the first alternative we must somehow account for an abrupt change from the bright *P. nokomis* to the dark *P. columbia*, for they do not intergrade to the extent to be expected if one arose from the other. A possible explanation is that at the time of adoption of the new host the insects were near to the parent stock in color and pattern, and the isolation due to the fact that the two major hosts do not exist together, in time, permitted the divergence to the present forms. In the alkaline section where the form *P. nokomis* is found, the *Platysamia* are brighter than in neighboring regions. It is a well established fact that the forms found in the alkaline deserts of the southwest are paler than similar forms in less humid, less alkaline regions. Whether this is indirectly due to the aridity or the alkalinity we do not know. In the species of Lepidoptera in which the inheritance of melanism has been worked out, it is on the whole dominant and caused by a small number of factors, so the dark *P. columbia* could develop from the parent stock in a relatively short time through mutation. A less likely explanation for the dark color lies in the observed fact that, particularly in the Geometridæ, the forms of Lepidoptera that feed on conifers tend to be dark.

The alternative that *P. columbia* arose from the main stem at a point north of the *P. nokomis* territory is rendered unlikely by the fact that *P. winonah*, the most northern form known, is even brighter than *P. nokomis*.

While there is complete hybrid intergradation in the northern zone of contact between *Platysamia gloveri* and *P. euryalis*, in the zones of contact between *P. cecropia* and *P. nokomis* or *P. columbia*, the change from one species to the other is rather abrupt, only traces of the influence of *P. cecropia* being present in *P. nokomis* and *P. columbia*. Since cross breeding occurs as freely in this zone of contact as in the other, and since the hybrids have been reared to maturity, the survival of the hybrids or secondary hybrids under normal ecological conditions must be extremely limited. This may be due to a wider physiological divergence between *P. cecropia* and *P. columbia* or *P. nokomis* than between *P. euryalis* and *P. gloveri*. This greater physiological di-

vergence in turn may be due to a longer period of isolation before contact was re-established.

We have established, it is hoped, the manner in which a genus composed of three lines of descent has diverged into six forms that have been described as species or subspecies. We have demonstrated that one of these forms (*P. kasloensis*) is a hybrid intergrade and that at least two others (*P. nokomis*, *P. columbia*) show hybrid influence. A question may be raised that we are not dealing with several species, but with forms of one species, with, in fact, a Rassenkreise or Formenkreise.²⁵ Into what classification does our group fit? Let us review briefly the various concepts of species in the Lepidoptera and the bases for their determination.

Man has always tried to classify the many and diverse forms of life into *discrete* groups. These groups he calls species. When the species determined on any particular basis, tend to intergrade so that it becomes difficult or impossible to fix the limits of any one, a new basis for differentiation is proposed.

The earliest basis for separation of species in the Lepidoptera was that of markings and the color of the vestiture. As long as collections remained small, this was held to be sufficient, but as more and more specimens were taken from more and more localities, the gaps between some of the species became filled in and new bases for differentiation became necessary or new concepts proposed. At the present time both avenues of escape are in use. One is the employment of the chitinous structure of the male or female genitalia as the criteria for differentiating species. As yet it has been possible to fit the material into this system, but as in the case of *Platysamia columbia*, examples will be found that do not conform. Another system is the conception of Rassenkreise or Formenkreise in which the various local races of a diverging group are placed together in a sort of super species. The basis of differentiation is physiological unity, the standard of measurement being the tendency to pair.

In the group of forms studied in this work there is considerable intergradation in color and pattern, so much that speciation must be made partly on the basis of locality and the lines of division become arbitrary and inconsistent. Similarly the very minute differences in

²⁵Goldschmidt, Richard. "Some Aspects of Evolution," *Science*, Vol. 78, p. 539. 1933, and Stresemann, Erwin. "Scientific Nomenclature," *The Auk*, Vol. XLI, 1924.

genitalia are intermediate in the zones where color and pattern intergrade. The forms freely interbreed and the offspring can be reared to the imago. If this were all, the entire genus would make an excellent Formenkreise, *but the female hybrids are all sterile*, and the continuance of the hybrid race dependent on backcrossing to the parent species by the males. This fact makes it impossible that the various forms be included under a single species or super species such as a Formenkreise, because, while the production of fertile hybrids is no longer prima facie evidence that the interbreeding forms are the same species, the failure to produce any fertile females remains a definite basis for their separation.

The genus *Platysamia*, then, is neither a group of separate, distinct species nor a Formenkreise of geographic races. It is half way between. It is not even homogenous in this respect, for *P. euryalis* and *P. gloveri* are nearer to the Formenkreise concept than *P. nokomis* and *P. cecropia* or *P. columbia* and *P. cecropia*.

We are forced to include the past history of the insects and return to the concept that all living forms merely represent the present day cross section through the development and differentiation of life through the ages. In this concept, the distinct species or the Formenkreise are merely accidents dependent upon where the cross section is made. The analogy of the tree admirably illustrates the idea. In this analogy the discrete species would be the ends of branching twigs that were cut at some distance from the fork, while the Formenkreise would be the ends of the twigs if cut as close to the fork as possible.

But the concept of the twig alone illustrates only one phase of the divergence. Often two forms may be morphologically distinct but physiologically alike as in the case of subspecies and the various groups of a Formenkreise. These forms or subspecies freely interbreed and produce fertile offspring. Usually physiological differentiation lags behind morphological differentiation so we may diagram it by surrounding the twigs representing the related forms by larger cylinders.

We find cases like the *Platysamia* in which the forms may interbreed naturally but produce offspring with varying degrees of fertility. The extreme limit of production of hybrids fertile to any degree may be represented by a still larger cylinder. The picture would then be like the bottom part of figure 5.

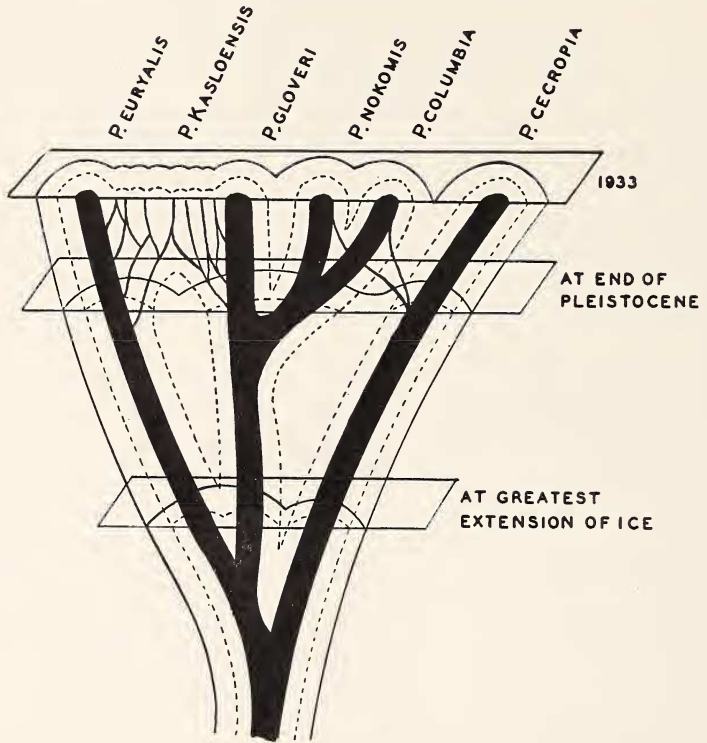
To represent the conditions in the Lepidoptera more exactly it

would be necessary to replace the sharply defined cylinders of the illustration with ones that become progressively weaker and more diffuse as the distance from the axis increases. The relative sizes of the cylinders may be varied to fit the characteristics of the forms studied. Often the cylinder representing the limit of fertility will coincide with that indicating physiological divergence. Sometimes, as in the case of insects specialized to diverse food plants without morphological change, the cylinder representing physiological divergence will be smaller than that showing morphological differentiation. On the whole, the relative proportions will be much as indicated in the diagram.

If the above analogy gives a true picture of the manner in which evolution is taking place in the Lepidoptera, then there should be found groups varying from isolated monotypic genera, through genera composed of single aggregations of subspecies, through the single *Formenkreise*, through intermediate phases such as shown by the *Platysamia* to genera composed of discrete species; from there to genera made up of groups of subspecies or *Formenkreises*, depending on at what level in the differentiation the present geological moment cuts the family tree. Such a gradation can be shown by groups selected from the North American fauna. The monotypic genus may be represented by *Macronoctua onusta*, the group of subspecies by *Parasemia Plantaginis*, the intermediate group by the *Platysamia*, the genus of discrete species by the genus *Vanessa* and the genus composed of a number of aggregates of subspecies by the genus *Argynnis*.

If we analyze the genus *Platysamia* on the basis of the augmented twig concept, we get a diagram as in figure 5. We find that while the forms may be distinct morphologically and physiologically, they are not separated beyond the point where hybrid intergradation can occur. That this hybridization has occurred is indicated on the diagram by the converging lines.

What shall we call the hybrid intergrade? If we give a name to the primary hybrid, we must give another name to the secondary hybrid, etc. This is further complicated by the fact that the various hybrid broods having the same species as parents differ greatly. In the case of the *Celerio galli* x *C. euphorbiae* crosses there are at least eleven names applied to the various hybrids. If the crossings of these two species occurred in nature and all of the various hybrid intergrades flew together as do the *Platysamia gloveri* x *P. euryalis* inter-



PHYLOGENETIC TREE OF THE PLATYSAMIA

FIG. 5. Reproduced from "University of Pittsburgh Bulletin" (Graduate School Abstracts, Vol. X), Vol. 31, 1934, p. 353.

grades, it would be impossible to apply the proper names to the specimens caught. The problem has been solved for the natural hybrid intergrades by Lotsy²⁶ who applies one name to the entire intergradation. According to his system the *euryalis-gloveri* intergrades would be called *Platysamia kasloensis populus hybridogenus* or abbreviated *Platysamia kasloensis p. h.*

VI. CONCLUSIONS

1. The genus *Platysamia* as analyzed here is an excellent example to illustrate the futility of attempting to set up rigid universal criteria

²⁶Lotsy, J. P. and Goddyn. "Voyages of Exploration to Judge of the Bearing of Hybridization upon Evolution." *Genetica*, Vol. 10, 1928.

for defining the limits of species or other taxonomic concepts even for such relatively homogeneous groups as the Lepidoptera.

2. Intergrades can and do arise in nature through the process of hybridization.

3. Intergradation through hybridization is not necessarily the same as the hybridization that occurs during and after the differentiation of one subspecies from another, because, as in the case presented, there may not be complete fertility between the parent stocks.

4. Without a knowledge of the geologic history of the forms studied it would be difficult, if not impossible, to distinguish between hybrid intergradation and the transition stages between geographical subspecies, for these transition stages necessarily involve hybridization.

5. *Platysamia kasloensis* is not a true species or subspecies but a hybrid aggregate, an example in the Animal Kingdom of the "populus hybridogenus" of Lotsy. It is a definite, naturally occurring group of animals and must therefore be recognized in systematic zoology, but not as species, subspecies or variety.

6. Hybridization is an excellent tool for the analysis of intergrades and for the determination of the relative physiological divergence between species.

VII. APPENDIX I

THE ORIGINAL DESCRIPTION OF THE GENUS SAMIA—HÜBNER, 1816²⁷

2 Verein	Coitus 2.
Samien	Samia

Die Mittezierde aller flugel sehr nachlassig, aber am Ende der Schwingen ein deutlicher Schwarzes. Ungen: fleetken

1629 Samia Cynthia Cramer 39a

1630 Samia cecropia Cramer 42 AB

1631 Samia Promethea Cramer 76 AB and 75 AB

WALKER'S REDESCRIPTION OF THE GENUS SAMIA, 1855²⁸

Samia Hübner Verz Schat. 156

Phalana Attacus P. Linn., etc.

Bombyx P. Fabr.

Hyalophora P. Duncan Nat. Libr. VII

Saturnia, P. Westwood

²⁷Hubner, Jacob, *Verzeichniss Bekannter Schmetllinge*, 1816.

²⁸Walker, *Catalogue of Lepidoptera Heterocera in the Collections of the British Museum*, 1855.

Male body hardly stout. Antennæ very deeply pectinated; branches of equal length, slender, ciliated, in pairs. Abdomen extending to about one-third of the breadth of the hind wings. Fore wings falcate at the tips, undulating and very oblique along the exterior border; interior angle rounded; discal areolet open; three inferior veins; first and second contiguous; third very remote. Hind wings very much broader than the fore wings. Female.—Body stout. Antennæ deeply pectinated, otherwise like those of the male. Abdomen extending to half the breadth of the hind wings. Fore wings hardly falcate; exterior border much less oblique and undulating than that of the male. Hind wings not so broad.

In this genus the coloring of the wings much resembles in design that of *Attacus*, but the hind wings of the females are not dilated, and there is no trace of a vitreous spot.

1. *Samia promethea* Drury
2. *Samia auguliferi* Wlk.
3. *Samia cecropia* Linn.
4. *Samia calleta* Westwood.

THE ORIGINAL DESCRIPTION OF THE GENUS CALLOSAMIA, 1864²⁹

"CALLOSAMIA Nov. Gen."

"Front of the head narrow compared with *Samia* and not so hairy. Antennæ broadly pectinated, in female two-thirds as broad as in male. Mandibles obsolete. Maxillæ very short. Mentum and labrum coalesced, short and rounded in front, bearing the small short depressed cylindrical clavate palpi, which are thinly clothed with long scales. Fore wings more than twice the length of the whole body, falcate. Hind wings much produced at the anal angle. The first median nervule in the primaries subdivides a little beyond its origin.

"I should here state that soon after beginning my studies upon this family, Professor Agassiz indicated to me that *S. promethea* should form the type of a separate genus from *Samia*.

"Differs from *Samia* in its lighter form, more falcate primaries, in having the hind wings much longer behind, while in the middle of the wings are partially transparent triangular spots."

"*Callosamia promethea*"

"*Callosamia augulifera*"

²⁹Packard, A. S. "Synopsis of the Bombycidæ of the United States, Part II." *Proceedings of the Entomological Society of Philadelphia*, Vol. 3, pp. 379-380, 1864.

ORIGINAL DESCRIPTION OF THE GENUS PLATYSAMIA—GROTE, 1865³⁰

"PLATYSAMIA Nov. Gen."

"The clypeus, which is narrower than in *Samia* and broader than in *Callosamia* is clothed with longer hair which descends downward, hiding the very small labial palpi, still further hidden by an inferior long tuft of hair. Maxillæ wanting. Head small and sunken into prothoracic parts. The antennæ are long and strongly bipectinate. In the male the pectinations are full twice as long as in the female and densely ciliated. Mesothorax broad and stout, longly and loosely haired. Abdomen stout, and heavier and longer than in *Samia*. Wings broad and ample; primaries hardly falcate, since there is a very slight depression in the external margin at the extremity of the third s. c. nervule. Nervules long and arcuate; third s. c. arcuate (thus opposed to *Samia*) so also the second median nervule. Discal space centrally narrower than in *Samia*; sub-costal nervure bent downward at base. Secondaries broad and ample; external margin rounded; anal angle less prominent than in either *Samia* or *Callosamia*. The neuration of the secondaries affords distinct differences compared with *Samia*, particularly in the course of the median nervules which are more bent. The species are:

Platysamia cecropia Linn.

Platysamia columbia Smith

Platysamia californica Nov. Sp."

³⁰Grote, A. R. "Notes on the Bombycidæ of Cuba," Proceedings of the Entomological Society of Philadelphia, Vol. 5, pp. 227-229 (1865).

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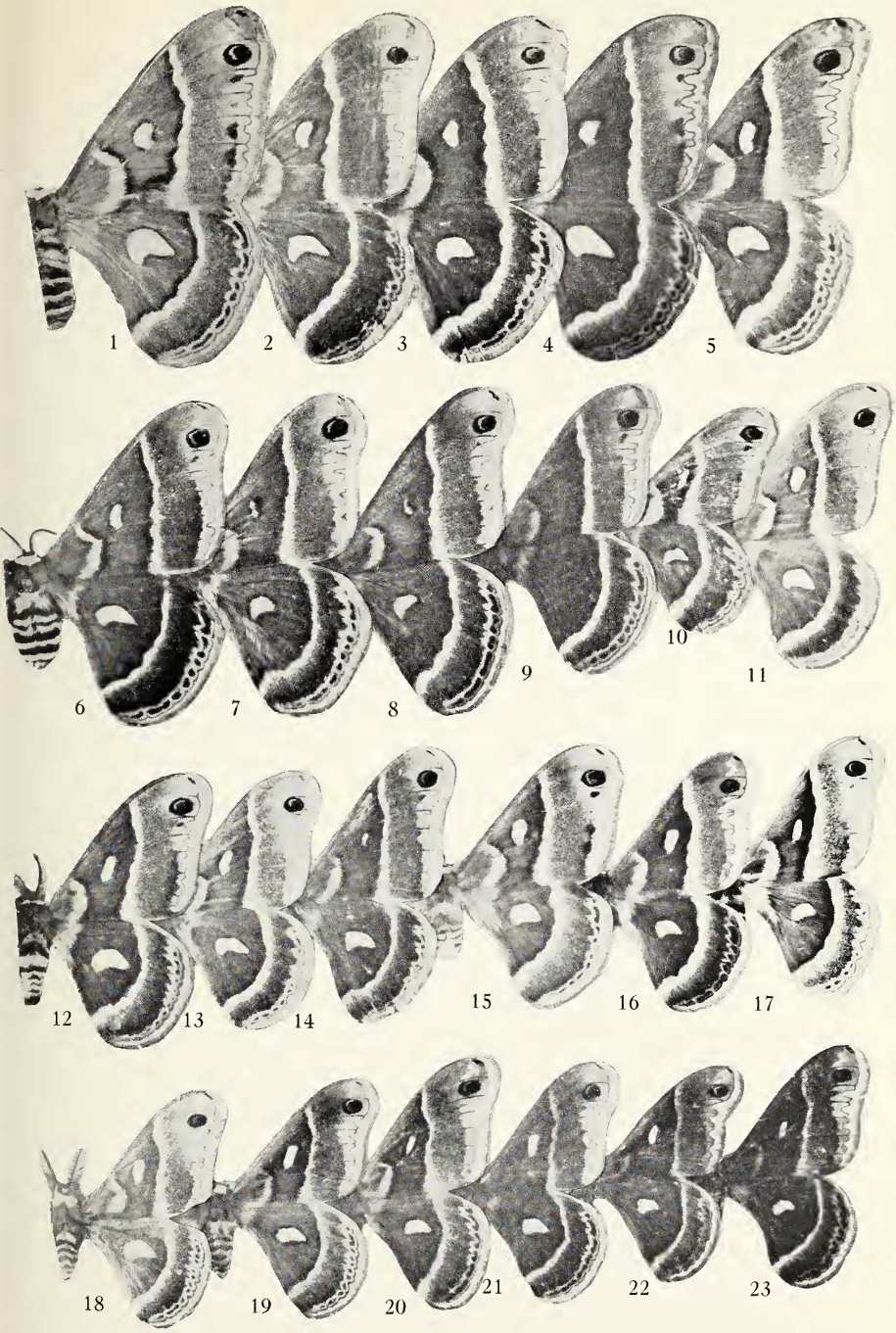
1. *Platysamia gloveri* ♂, Salt Lake County, Utah.
2. " " ♂, Springdale, Utah.
3. *Platysamia cecropia* ♂, Pittsburgh, Pennsylvania.
4. " " ♀, Dickinson, North Dakota.
5. " " ♂, Pittsburgh, Pennsylvania, normal form.
6. *Platysamia* hybrid (*cecropia* ♂ x *gloveri* ♀) ♀.
7. *Platysamia euryalis* ♀, Bred from San Francisco, California, stock.
8. *Platysamia columbia* ♂, Whitemouth, Manitoba.
9. *Platysamia nokomis* ♂, Miniota, Manitoba.
10. " " ♂, Two Creeks, Montana.
11. *Platysamia kasloensis* ♂, Lookout Pass, Mineral County, Montana.
12. " " ♂, Martina, Montana.
13. " " ♂, Lookout Pass, Mineral County, Montana.
14. " " ♂, Martina, Montana.
15. " " ♂, Martina, Montana.
16. *Platysamia gloveri*? ♂, Helena, Montana.
17. *Platysamia* hybrid (*cecropia* ♂ x *gloveri* ♀) ♂.
18. " " (*gloveri* ♂ x *cecropia* ♀) ♀.
19. " " (*columbia* ♂ x *gloveri* ♀) ♀. Pattern somewhat diffused
because of exposure to cold.
20. " " (*cecropia* ♂ x *gloveri* ♀) ♂. No red in extradiscal band.
21. " " (*gloveri* ♂ x *cecropia* ♀) ♀.
22. " " (*euryalis* ♂ x *cecropia* ♀) ♂.
23. " " (*nokomis* ♂ x *cecropia* ♀) ♂ ♀.
24. " " (*columbia* ♂ x *cecropia* ♀) ♂.
25. " " (*columbia* ♂ x *cecropia* ♀) ♀.
26. " " (*nokomis* ♂ x *cecropia* ♀) ♂.
27. " " (*nokomis* ♂ x *cecropia* ♀) ♀.



EXPLANATION OF PLATE XVI

VARIATION IN THE GENUS PLATYSAMIA

1. *Platysamia gloveri* ♀, Temecula, California.
2. " " ♂, Arizona. Not quite typical, discal spot too short.
3. " " ♀, Fort Wingate, New Mexico.
4. " " ♀, Salt Lake County, Utah.
5. " " ♂, Salt Lake County, Utah.
6. " " ♀, Salt Lake County, Utah.
7. " " ♂, Salt Lake County, Utah.
8. " " ♂, Salt Lake County, Utah.
9. " " ♂, Bradley, Montana.
10. " " ♂, Helena, Montana.
11. " " ♂, Helena, Montana.
12. " " ♂, Salt Lake County, Utah.
13. " " ♂, Gold Creek, Montana.
14. " " ♂, Custer, South Dakota.
15. *Platysamia nokomis* ♀, Miniota, Manitoba.
16. " " ♂, Miniota, Manitoba.
17. " " ♂, Two Creeks, Manitoba.
18. " " ♂, Miniota, Manitoba. Showing whitish suffusion.
19. *Platysamia columbia* ♂, Whitemouth, Manitoba. Light form.
20. " " ♂, Whitemouth, Manitoba.
21. " " ♂, 12 miles north of North Bay, Ontario.
22. " " ♂, Whitemouth, Manitoba.
23. " " ♂, Whitemouth, Manitoba. Practically black.



EXPLANATION OF PLATE XVII

VARIATION IN THE GENUS PLATYSAMIA

Figures 1 to 14 show the variation in the shape of the discal spot in the form *P. kasloensis*.

1. *Platysamia kasloensis* ♂, Pine Creek, Shoshone County, Idaho.
2. " " ♂, Lookout Pass, Montana.
3. " " ♂, Lookout Pass, Montana.
4. " " ♂, Lookout Pass, Montana.
5. " " ♂, Martina, Montana.
6. " " ♂, Pine Creek, Shoshone County, Idaho.
7. " " ♂, Cabin City, Mineral County, Montana.
8. " " ♂, Martina, Montana.
9. " " ♂, Lookout Pass, Montana.
10. " " ♂, Lookout Pass, Montana.
11. " " ♂, Enaville, Idaho.
12. " " ♂, Pine Creek, Shoshone County, Idaho.
13. " " ♂, Lookout Pass, Montana.
14. *Platysamia gloveri* ? ♂, Helena, Montana.
15. *Platysamia euryalis* ♀, Middle California. Shows extreme length of discal spot.
16. " " ♂, Reno, Nevada.
17. " " ♂, Middle California.
18. *Platysamia cecropia* ♀, Pittsburgh, Pennsylvania. Aberration caused by cold.
19. " " ♀, Dickinson, North Dakota. Extreme red form.
20. " " ♀, Riding Mountains, Manitoba. Probably secondary hybrid.
21. " " ♀, New York. Normal.
22. " " ♂, New York. Red band practically absent.
23. " " ♂, Martin River north of North Bay, Ontario.
24. " " ♂, Ninette, Manitoba.
25. " " ♀, Pennsylvania. Extremely dark form.
26. " " ♀, Pennsylvania.

